SHOUT
SHARE
IT

MUS
4890

HARVARD UNIVERSITY

LIBRARY

OF THE

Museum of Comparative Zoology

BULLETIN

OF THE

MUSEUM OF COMPARATIVE ZOÖLOGY

AT

HARVARD COLLEGE, IN CAMBRIDGE.

VOL. XXXI.

LIBRARY
MUS. COMP. ZOÖLOGY
CAMBRIDGE, MASS.

CAMBRIDGE, MASS., U. S. A.
1897 – 1898.

Reprinted with the permission of the original publisher
KRAUS REPRINT CORPORATION
New York
1967

S-NA-C

Printed in U.S.A.

CONTENTS.

Page

No. 1. — Contributions from the Zoölogical Laboratory. LXXXIII. Contributions to the Morphology of the Turbellaria. II. On some Turbellaria from Illinois. By W. McM. Woodworth. (1 Plate.) October, 1897 1

No. 2. — On the Relations of certain Plates in the Dinichthyids, with Descriptions of New Species. By C. R. Eastman. (5 Plates.) October, 1897 17

No. 3. — Contributions from the Zoölogical Laboratory. LXXXIV. Trichonympha, and other Parasites of Termes Flavipes. By J. F. Porter. (6 Plates.) October, 1897 45

No. 4. — Contributions from the Zoölogical Laboratory. LXXXV. Variations in the Brachial and Lumbro-Sacral Plexi of Necturus Maculosus Rafinesque. By F. C. Waite. (2 Plates.) November, 1897 . . . 69

No. 5. — Reports on the Dredging Operations in the "Albatross" in 1891. XXII. The Isopoda. By H. J. Hansen. (6 Plates and Chart.) December, 1897 93

No. 6. — Contributions from the Zoölogical Laboratory. LXXXVII. The Thoracic Derivatives in the Postcardinal Veins in Swine. By G. H. Parker and C. H. Tozier. March, 1898 131

No. 7. — Contributions from the Zoölogical Laboratory. LXXXIX. The Segmentation of the Nervous System in Squalus Acanthias. A Contribution to the Morphology of the Vertebrate Head. By H. V. Neal. (9 Plates.) May, 1898 145

Bulletin of the Museum of Comparative Zoölogy
AT HARVARD COLLEGE.
Vol. XXXI. No. 1.

CONTRIBUTIONS TO THE MORPHOLOGY OF THE TURBELLARIA.

II.

ON SOME TURBELLARIA FROM ILLINOIS.

By W. McM. Woodworth.

With One Plate.

CAMBRIDGE, MASS., U. S. A.:
PRINTED FOR THE MUSEUM.
October, 1897.

No. 1. — *Contributions to the Morphology of the Turbellaria.*

II.

On some Turbellaria from Illinois.[1] By W. McM. Woodworth.

The material upon which this paper is based was collected by the staff of the Biological Experiment Station of the Illinois State Laboratory of Natural History at Havana, Illinois, and came from the Illinois River and the streams and lakes tributary to it.[2] The material was collected between the first of July and the last of October, 1894, and the first of March and the last of September, 1895. I am indebted to Prof. S. A. Forbes, Director of the Illinois State Laboratory, for the privilege of studying the collections, and am under obligations to Dr. C. A. Kofoid, Superintendent of the Experiment Station, and to Prof. Frank Smith for their patience and kindness in answering my many inquiries, and for sending me living material from time to time. I must thank these gentlemen also for the excellent state of preservation of all the material that came into my hands.

Although I have to report but two species that are probably new, it is hoped that these pages will help to clear away some of the confusion that exists in the published accounts of the North American fresh-water Turbellaria. Although the figures accompanying this paper do not, with two exceptions, represent new forms, they are, I believe, the first published illustrations, in the natural colors of the living animals, of some of our common fresh-water Turbellaria.

I have not entered into the finer anatomy of the species to any extent, as that would have been beyond the scope of the paper. Unfortunately, too, not all of the species were represented by sexually mature individuals, and as the characters of the sexual organs are of the highest systematic importance, the unavoidable lack of data upon this subject must necessarily leave my work more or less incomplete. It is to be regretted also that living material could not be had of all the species treated of, as descriptions based solely upon alcoholic material are, to say the least, unsatisfactory, owing especially to the effect of reagents upon the pigments.

---

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, E. L. Mark, Director, No. LXXXIII.

[2] For a description of the localities under investigation by the Experiment Station, see C. A. Hart, On the Entomology of the Illinois River and adjacent Waters. Bull. Ill. State Lab. Nat. Hist., Vol. IV. p. 150, 1895.

The collections comprise five (?) species of Triclads and two Rhabdocœls. Three of these I hope to show are cosmopolitan in their distribution.

Dendrocœlum lacteum Oersted.

Figures 1, 9-15.

Dendrocœlum lacteum Oersted, 1844, p. 52. Woodworth, 1896^b, p. 1048.
Dendrocœlum superbum Girard, 1851, p. 265; 1851^a, p. 2.
Dendrocœlum superbum Leidy (non Girard), 1852^b, p. 288.
Dendrocœlum pulcherrimum Girard, 1851, p. 265; 1851^a, p. 2.
Procotyla fluviatilis Stimpson (Leidy MS.), 1857, p. 23. Diesing, 1862, p. 517. Leidy, 1885, p. 51. Hallez, 1890, p. 105. Girard, 1893, p. 164. Woodworth, 1896, p. 95; 1896^a, p. 241.[1]
Procotyla leidyii Girard, 1893, p. 166.

Station C; 13,166, "small pool on sandy margin of Thompson's Lake near Station G."

Color, milk white; creamy, yellowish, or, in larger, older specimens, roseate; no pigment except in eye-spots. Very translucent; intestine in all its ramifications easily seen, grayish to brown or black according to the character of the contents, more deeply colored in larger specimens. A slight constriction immediately behind the plane of the eyes, marking off an anterior head end and producing the lateral projecting rounded cephalic appendages. Gradually widening posteriorly from constricted or neck region to a point about one sixth the total length from the anterior end, then margins are parallel to about one fifth the distance from the posterior end, tapering gradually from this point to the rounded posterior extremity. When in active motion and fully extended, the lateral margins are smooth and nearly parallel; but when partly contracted or at rest, the margins are very sinuous or crenate and thrown into folds, like the margins of many marine Planarians. A well marked median adhesive disk or sucker at the anterior end, the diameter of which is about one third the broadest diameter of the head. When the animal is in motion the shape of the anterior end is continually changing, owing to the protrusive and retractive movements of the disk, which can be protruded for a considerable distance, though projecting only slightly when in the retracted condition. Eyes usually two, but frequently accessory eye-spots from one to six in number. Distance between the eyes a little greater than from eyes to margin of head. Mouth opening (in preserved material) slightly posterior to a point midway between anterior and posterior ends. Gonopore (in preserved material) two sevenths of the total length from the posterior end. Length from 10 to 22 mm.; greatest breadth from 2 to 3 mm.

---

[1] By a gross error I have in the above paper also referred to Keller und Tiedemann's Nordamerik. Monatsber. for 1851.

Dendrocœlum lacteum, which is one of the commonest and most widely distributed of European fresh-water Planarians, has often been the object of study, and its structure is better known, perhaps, than that of any other Triclad. Chief among the papers dealing with this species is that of Iijima (1884); our American form agrees so closely with his account that a discussion of the finer anatomy of the species will not be entered into here, except in so far as regards the anterior adhesive disk, and some points in connection with the male sexual organs; for other details the reader is referred to Iijima.

It is remarkable that Iijima should have overlooked the adhesive disk of *D. lacteum*. Though he states (p. 362) that he did not find the organ, two of his Figures (Taf. XXII. Figs. 9 and 10) are very suggestive, and coincide with similar preparations of my own. The organ was seen by von Baer (1827, p. 715), who describes it as a "kleine Pupille"; Dugès (1828, p. 150) also speaks of it as "un renflement qui peut aisément se creuser en cupule, en ventouse semblable à celle de la queue des sangsues et la face inférieure des Douves," and he shows it in his Fig. 7, Pl. 4. Leydig (1864) figures it (Taf. I. Fig. 2), and in his account of its structure mentions the absence of rhabditi and cilia in the cells lining the depression. The organ is characteristic of the genus Dendrocœlum, and occurs in every other species of the genus whose structure has been investigated. The failure of Iijima to find the organ is explained by Weltner (1887, p. 800) as being due to the great variability of the organ itself in the same individual, depending upon different phases of contraction and expansion, it being at times difficult to recognize it. The variability in the shape of the disk was also referred to by Leydig (*loc. cit.*), and Girard (1893, Pl. 4) figures many phases of its activity. I also can testify to the great mobility of the adhesive organ, and to its varying prominence in the same and in different individuals.

As a rule, it is more prominent in the largest, oldest individuals; in those 10 mm. and under in length, I have often had considerable difficulty in recognizing it even in sections, there being nothing to replace it but a shallow groove. Figures 13–15 are from sections of an individual of the largest size, and represent the organ in an exceptionally prominent condition. The organ cannot be compared to the sucker of cotyligerous Turbellaria, or to the muscular sucking disks of other Platyhelminths, nor to that of the leech; it lacks the special musculature often so elaborately developed in these. It is simply a depression at the anterior end of the animal into which open the numerous mucous glands which in most Triclads are found in this region. It is comparable, rather, to the frontal organ of the Acœla, and more particularly to the organ existing at the anterior end of *Mesostoma lingua*, which has been described and figured by Graff (1882, p. 288). In this species the pit is formed by the inversion of that part of the anterior end where the two great tracts of rhabditi ("Stäbchenstrassen") open to the exterior, and according to Graff is not permanent or constant. I have elsewhere (1891, p. 23) expressed my belief in the homology of the "Stäbchenstrassen" of the Rhabdocœls with the cephalic slime glands of Triclads, and a comparison of the sagittal section of *M. lingua* (Graff, 1882, Taf. VI. Fig. 3) with Figure 15 of this paper is strikingly suggestive in this regard. Kennel (1888, p. 455) has also shown that in many fresh-water Triclads there appears in preserved material a more or less shallow groove, or depression, on the ventral surface at the anterior end corresponding to a region by which the living animals are able to attach themselves. It is the region where the cephalic slime glands open to the exterior. He suggests for the ridges at the sides of these ventral depressions the names "Haftwulsten" and "Haftlappen." Grube (1872) has also described similar pits or grooves in several fresh-water Planarians.

The organ in *D. lacteum* is not a true sucker, nor does the animal employ its anterior end for the purposes of attachment to any greater degree than the posterior or lateral margins of its body, along the ventral surface of which numerous mucous glands have their openings. In truth, it is the margins and posterior end that adhere more firmly to a support; often when the animal is forcibly removed from the side of the aquarium the parts of the margin or the posterior end will adhere so firmly to the glass that the points of attachment are drawn out into digitate processes. Figures 13 and 14 are from transverse sections through the adhesive pit of *D. lacteum*, Figure 13 being through the almost extreme anterior part, while Figure 14 is somewhat more posterior. Both sections are from the same individual, — one in which the organ was unusually well developed. Figure 15 represents a sagittal section through another individual, and Figure 9 is a surface drawing of an individual killed in hot corrosive sublimate. It will be seen that the region involved in the organ embraces all that portion of the hypodermis occupied by the openings of the mucous glands. As already shown by Leydig (1864), the hypodermis which lines the depression is devoid of cilia and rhabditi, the latter being replaced by the mucous glands, and the transition from one to the other being gradual. The exact histological character of the hypodermis lining the depression could not be ascertained, the terminal ducts of the glands being so closely compacted as to mask all details in this region. In Figures 14 and 15 are seen cross and longitudinal sections of the retractor muscle of the organ. Nothing in the shape of a protractor muscle could be discovered, this function possibly being assumed by the circular muscles of the dermo-muscular sac.

The variation in the number of the eye-spots is not a feature peculiar to the American form of *D. lacteum*, as I stated in a previous note (1896^b, p. 1048), for accessory eyes, "Nebenaugen," have been observed in this species by Carrière (1882, p. 164) and Iijima (1884, p. 438), according to whom they are not rare. According to my observations there is in such cases usually one pair of eye-spots, corresponding to the normal single pair, which is more prominent than the accessory eye-spots. In what appears to be a closely allied form, *Sorocelis gutata* Grube (1872), there exist two series of eye-spots arranged in the form of two arcs; the number of eyes in each arc is usually seven, but there may be as few as two, nor is the number always the same on both sides. I have never observed more than a total of eight eye-spots in *D. lacteum*, there being from one to six accessory eyes, either equally or unequally distributed on the two sides of the head. Girard (1893, p. 165) describes and figures variations in the number of the eyes, and also shows the accessory eyes to be smaller than the pair of normal eye-spots. Leidy (1885, p. 50) also speaks of the accessory eyes. Of the many Illinois specimens of *D. lacteum* that have come under my observation, 33 per cent of the individuals exhibited variations in the number of the eyes.

Anastomoses in the branches of the intestine exist in most of the specimens examined; these are usually confined to the branches of the posterior trunks, which are often united by transverse commissures. In one case there were three such transverse commissures. Girard (1893, Pl. 4) figures an individual in which the posterior trunks can no longer be recognized as such, the digestive tract existing as a meshwork or reticulum. Leidy (1885, p. 50) and Iijima (1884, p. 390) also mention anastomoses, and the latter figures a commissure uniting the posterior trunks, while Wheeler (1894, p. 176), in a species which he believed to be *D. lacteum*, failed to detect any such connections. Hallez (1892) also figures such connections for this species.

I have little to add to the account of the sexual organs given by Iijima, but do not find the penis to be so nearly spherical in shape as that figured by him. The shape of the male organ is more like that figured for *D. lacteum* by Schmidt (1861, Taf. IV.), longer and more cylindrical. Nor is the cavity of the penis so large as that figured by Iijima, the muscular walls being much thicker (Figs. 10–12). The cavity of the penis is lined with a glandular epithelium, which projects into the lumen of the organ in folds, thus producing a large secreting surface. It is possible, of course, that the cavity varies at different periods of sexual activity. In one important particular only do my observations on the sexual organs differ from those of Iijima. According to that author the vasa deferentia open separately and directly into the cavity of the penis and at considerable distance from each other. My observations do not confirm the existence of such conditions, but show that the vasa deferentia unite into a slender ductus ejaculatorius, which extends in the longitudinal muscles of the organ along its ventral surface to that point where the penis begins to taper off to form the slender distal free intromittent part of the organ (Fig. 10). At this point, which may be designated as the root of the penis proper, and corresponds with the posterior limit of the glandular cavity, the duct becomes confluent with the cavity of the penis. In other words, the glandular cavity of the penis may be said to pour its secretions at this point into the seminal duct, and the greater mass of the penis can be compared to a prostate gland, the Körnerdrüse of Polyclads. In transverse section it is often difficult to follow the course of the duct, owing to its small size and to the fact that the lumen is often obliterated by the approximation of its walls, and frequently lies in one of the glandular folds projecting into the cavity of the organ (Fig. 12). The sheath of the penis in its deeper portions is thrown into many folds to provide a greater surface for the glands that secrete the shell of the cocoon (Fig. 11). These glands are spoken of by Iijima, but are not figured by him.

In a recent paper I (1896^b, p. 1048) have discussed the synonymy of Leidy's *Procotyla fluviatilis* and expressed my belief in the identity of this species with *Dendrocœlum lacteum;* upon the evidence presented above, I wish to emphasize my conviction in this regard. The apparent differences between the forms are in the American form the possible greater prominence of the frontal adhesive organ, the more frequent variation in the number of the eyes, and the separation of the seminal duct from the glandular part of the male sexual organ. The first two of these differences, as I have endeavored to show, are differences in degree only, and have no systematic value. The discrepancy between my account of the male sexual organs and that of Iijima alone stands as a real difference. Although I can find no account of anything similar in other Triclads, there are conditions comparable to these in the male organs of Polyclads and Rhabdocœls (Lang, 1884, and Graff, 1882), and it is possible that this detail has hitherto been overlooked in Triclads.

Neither have I any hesitancy in placing under *D. lacteum* Girard's *D. pulcherrimum* and *D. superbum.* The former differs, he says (1851, p. 265), from *D. lacteum* "by having three pairs of eyes instead of two," while his *D. superbum* (1851^a, p. 2) "gleicht vielleicht noch mehr als die vorgehende Art [*D. pulcherrimum*] den *D. lacteum*, wovon es sich unterscheidet durch kleinere dünnere Gestalt, zwei Paar Augen, vorstehendere Hörner und rothe oder milch weiss Farbe." It is significant, too, that Leidy (1852^b, p. 288) should have first ascribed his *Procotyla fluviatilis* to Girard's *D. superbum* (see Woodworth, 1896^b, p. 1048), and that Girard, in his recent extended monograph of North American Turbellaria, makes no mention of these two old species of his.

Planaria gonocephala Dugès.

Figure 5.

Planaria gonocephala Dugès, 1830, p. 83.

Planaria gonocephaloides Stimpson, 1857, p. 23. Diesing, 1862, p. 498. Silliman, 1885, p. 69.

Dugesia gonocephaloides Girard, 1851, p. 265; 1851^a, p. 2; 1891, p. 183.

Sides parallel, tapering gradually posteriorly to a rounded point. Anterior end obtusely pointed, angular, the sides of the head making an angle of about 60°. Two angular cephalic appendages. In alcoholic material the auricles are not prominent, scarcely showing at all in some specimens. Length of head about $\frac{1}{10}$ of the total length of the animal. Eyes two, in a plane joining the apices of the auricles. Clear area surrounding the eyes sometimes elongated in the antero-posterior direction. Color, dark reddish brown to grayish brown, uniform. Posterior margins of auricular appendages free from pigment. Length 9 to 15 mm., greatest breadth $\frac{1}{2}$ to 2 mm. (Two alcoholic specimens, which must have measured 20 mm. or more in length when alive.)

11,664*b*, Station C; 13,069, Station C.

Only one of the specimens exhibited sexual organs. There is no copulatory bursa and the oviducts open separately into the vagina immediately before it enters the genital atrium. The species in every way agrees with descriptions of the European form. There can be no doubt that it is the species described by Girard as *Dugesia gonocephaloides*. According to this author the latter differs from *P. gonocephala* only in the elongated form of the clear areas surrounding the eye-spots, and upon this meagre difference is founded the genus which Girard afterwards (1891) extended to include all forms bearing angular cephalic appendages. Stimpson and Diesing retained the specific name, but placed it under the genus Planaria, a fact that was apparently unknown to Silliman, who renamed it *Planaria gonocephaloides*. Hallez (1890, p. 78) has discussed the value of Girard's genus Dugesia, and places *D. gonocephala* as a synonym of *P. gonocephala*, in which species the elongated shape of the periocular areas is not uncommon. *P. gonocephala* has been shown by Iijima (1890, p. 338) to be cosmopolitan in its distribution, as it was found by him in Japan.

The color of the American representatives of *P. gonocephala* differs from that of the European in being of a deeper hue. The European forms vary from a gray to a brownish green, while the Illinois specimens are of a deep brown, which is well reproduced in Figure 5. Some specimens from France that I have received through the kindness of Professor Hallez, of Lille, are almost white in the alcoholic condition. Girard (1893, p. 183) describes the color of *Dugesia gonocephaloides* as often being a blackish brown.

Planaria dorotocephala, sp. nov.

Figures 4, 7.

Planaria maculata var. *a* Girard, 1893, p. 182.

Sides parallel, tapering gradually to a point posteriorly. Anterior end large, sharply pointed, the sides of the head making an angle of about 45° with each other. Two long sharply pointed, very prominent auricular appendages, slightly posterior to the plane occupied by the eyes. Auricles always prominent in preserved material. Length of head about $\frac{1}{6}$ of the total length of the animal. Width of the head at its junction with the auricular appendages greater than the diameter of body anywhere posterior to the appendages. Color, reddish to yellowish brown, uniform. Posterior margins of auricular appendages free from pigment. Occasionally a narrow light median streak extending caudad from just back of the eye-spots. Length 8 to 13 mm., greatest breadth $\frac{1}{2}$ to $1\frac{1}{2}$ mm.

22,081; Station H, Matanzas Lake; Station C; Havana.

A very active, restless, rampant form. When in motion the head is elevated and moved from side to side, the long auricular appendages being elevated above the head. After being disturbed, it does not come to rest for a long time as compared with *P. gonocephala* and *P. maculata*, the latter being particularly sluggish. A peculiarity of this species is the frequent occurrence of accessory posterior intestinal trunks, a condition that was present in fifty out of seventy-one specimens examined. In place of the two posterior trunks of the intestine, which exist in the ordinary Triclad type, there are often as many as three parallel trunks on each side of the pharyngeal chamber (Fig. 7). The accessory trunks either take their origin at the root of the pharynx, like the two normal posterior trunks, or exist as parallel branches of the latter, and usually unite with it and with each other close to their posterior terminations. I have never seen any anastomoses of the trunks of one side of the body with those of the other side, as in *D. lacteum.* When accessory trunks are present, they bear no lateral branches, but in place of these possess slight projections or buds, the lateral branches probably being suppressed through lack of space. The anterior portion of the intestinal tract, in almost every case where the specimens were not too heavily pigmented to be studied, exhibited anastomoses of the lateral branches, the intestine in some instances existing as a network (Fig. 7). (See under *D. lacteum*, *ante*, p. 2.) Unfortunately, I can say nothing in regard to the sexual organs of this species. In over one hundred individuals examined, not one was sexually mature or showed any signs of sexual organs.

Girard (1893, p. 181) describes three varieties of *Dugesia maculata.* The description he gives of his first variety, var. *a*, agrees closely with the form described above in size and shape, in color, in the frequent occurrence of the light median streak, in the greater length of the auricular appendages, and the more pointed shape of these and the head end. His Figure 56 also shows a third posterior trunk of the intestine, but median in position and anastomosing with the lateral trunks. There can be little doubt that var. *a* of Girard's *D. maculata* and *P. dorotocephala* are the same.

There is also a striking resemblance between *P. dorotocephala* and Kennel's figure of *P. aurita* (1888, Fig. 3).

Planaria maculata Leidy.

Figures 2, 3.

Planaria maculata Leidy, 1848, p. 251; 1848^{a}, p. 78; 1852, p. 225; 1852^{b}, p. 289; 1885, p. 50. Diesing, 1850, Vol. I. p. 205; 1862, p. 499. Stimpson, 1857, p. 23. Silliman, 1885, p. 70. Woodworth, 1896, p. 94; 1896^{a}, p. 240.
Dugesia maculata Girard, 1851, p. 264; 1851^{a}, p. 2; 1893, p. 181, var. *b* and *c*.
Planaria tigrina Girard, 1851, p. 264; 1851^{a}, p. 2; 1891, p. 179.

Anterior end pointed, sides of the head making an angle of about 60°. Two angular cephalic appendages. Length of head about $\frac{1}{10}$ the total length of the animal. Eyes two. Sides parallel to about $\frac{2}{3}$ of the total length from the anterior end, then tapering gradually to a rounded point. Color, blackish to purplish by reflected light; blackish or gray by transmitted light. In smaller young specimens, the pigment occurs in isolated patches and spots; in older specimens the pigment patches become more confluent, chiefly in the median region leaving clear irregular areas scattered over the surface of the animal.

Smaller spots of deep brown or black occur scattered over the surface among the larger patches. In the largest, oldest specimens there are very few or none of the clear areas. Frequently a light median streak more or less free from pigment occurs, extending backward from between the eye-spots (Fig. 3). Length 4 to 9 mm., greatest breadth ½ to 1½ mm.

Station D; 13,011, Station C; 13,113, Illinois R. at Havana; 22,050*a*, Station E; 13,521, Station L; 22,020, Station K; 22,033*d*, Station L; 22,011*c*, Station L; 22,053, Station H.

Planaria maculata is the commonest of our fresh-water Planarians and was the first one to be described (Leidy, 1848); however, nothing has been published regarding its sexual organs, and I am unable to offer anything in this regard; not one of the hundreds of specimens that came under my observation was sexually mature. The species, as already mentioned, is sluggish, seldom being in motion in the aquaria, and when stirred up in company with *P. gonocephala* and *P. dorotocephala* it is the first to come to rest. It is possible, as also suggested by Leidy (1885, p. 50), that it is nocturnal in its habits. It is usually found on the protected sides of stones, of empty Unio shells, or of aquatic plants, and often huddled together in large numbers.

About 40% of the Illinois individuals that I examined exhibited mutilations at the anterior or posterior ends, either by the absence of a head, or by being truncated posteriorly. In the cases where the posterior end is lacking the pharynx, instead of occupying a position midway between the anterior and posterior ends, extends almost to the posterior limits of the animal. There is no pigmentation about such scars. I have elsewhere (1896[a], p. 240) referred to the mutilations in *Planaria maculata*, and suggested that they were the result of reproduction by transverse division. I have since learned from Dr. Harriet Randolph that the species divides spontaneously, and that small fragments from any part of the body will regenerate into a new worm.[1]

---

[1] Through the courtesy of Dr. Randolph I am able to present the following table. The material upon which the experiments were made was collected on the island of Naushon, Vineyard Sound, Mass.

PLANARIA MACULATA. CASES OF FISSION.

Specimen.	Date of Isolation.	Kind of Water.	Date of First Fission.	Interval.	Date of Second Fission.
1	July 24	Rain	July 30		
2	July 24	Rain	August 1		
3	July 24 (?)	Rain	August 3	14 days	August 17
4	August 17 *	Lake †	August 21		
5	August 17 (?)	Lake †	August 25		
6	August 18	Spring	August 20		
7	August 17 or 18	Spring	August 26		
8	August 17 or 18	Spring	August 28		

* Whole number isolated on August 17 and 18 was forty individuals.

† From which the Planarians came.

Van Duyne (1896) experimented with a form which he states "war die *Planaria torva* von Wood's Holl." A study of his figures leads me to believe that the species used by him was *P. maculata*. I have found *P. maculata* to be very common at Wood's Holl and elsewhere on Cape Cod, where I have collected and where I have never met with a species that resembles in any way the *P. torva* of Europe ; nor has that species ever been described from the United States. In *P. torva* the head is not defined from the body by lateral cephalic appendages, the anterior end of the animal is simply rounded. The contrary is true of the species shown in Van Duyne's figures, where there is indicated a sharply marked angular head and well marked projecting cephalic appendages.

Many of the specimens showed dark spheroidal bodies scattered through the parenchyma, as many as fifteen of the bodies occurring in a single individual. In sections they proved to be small encysted Trematodes. The cysts measured from 0.025 to 1.1 mm. in diameter. I have also met with Trematodes in the mesenchyma of *Bdelloura parasitica*.

Borelli (1895) has called attention to the resemblance of his Paraguayan *P. dubia* to our *P. maculata* as described by Girard, and has named a variety of it *P. dubia* var. *maculata*.

Planaria unionicola, sp. nov.

Figure 8.

It is with considerable reserve that I offer a new species upon the meagre evidence at my disposal, but such data as there are cannot be reconciled with descriptions of any known species. There was but one specimen (13,646), which was much contracted and shrivelled. It was found creeping on the mantle of *Unio alatus*, dredged from deep water in the Illinois River near Havana, August 30, 1895. According to the collector's notes the general color of the animal was "brownish red . . . mottled with purplish dots." On an outline drawing evidently made from the living animal, and which is reproduced in Figure 8, the color is also indicated as "light brick red" and the "purple dots" as occurring "all over the surface in masses, except at the margins," the dotted line in the figure no doubt representing the limits. The red color is also noted as being absent over an elongated posterior median area extending nearly to the posterior end of the animal (Fig. 8). The head end has a sinuous outline, producing three lobes or rounded projections, a median anterior one and two lateral cephalic appendages. There are two eyes occupying the inner margins of large circular periocular spaces. The sides are nearly parallel, and the posterior end is abruptly rounded, so blunt, indeed, as to suggest an injury or that transverse division had taken place. If the clear median elongated space indicates the position of the pharynx, its extreme posterior position is also indicative of an injury or a division. The color of the alcoholic specimen was a deep rusty red. Owing to the crumpled condition of the specimen nothing of any internal organs could be recognized, even when subjected to the most powerful clearing reagents. The length of the specimen was 2.8 mm., the greatest breadth 1.8 mm. When alive the worm probably must have attained a length of from 8 to 10 mm.

Whether the occurrence of the animal on the mantle of Unio is an indication of a parasitic mode of life, like that of the Triclads of the genera Bdelloura (Leidy, 1852[a]) and Syncœlidium (Wheeler, 1894), or whether its occurrence was purely accidental, can only be determined by careful and extended search.

Mesostoma ehrenbergii O. Schmidt.

Figure 6.

Mesostoma ehrenbergii O. Schmidt, 1848, p. 47.
Mesostoma wardii Woodworth, 1896, p. 95; 1896[a], p. 241.

No. 13,521, Station L; No. 13,626, Illinois River.

In a report on the Turbellaria collected by the Michigan Fish Commission I (1896, 1896[a]) described what I believed to be a new species of Mesostoma under the name of *M. wardii*, basing the species chiefly upon the uniformly small size and the absence of cephalic tracts of rhabditi or "Stäbchenstrassen." A comparison, however, with a larger number of Illinois Mesostoma has convinced me of the identity of both the Michigan and Illinois forms with *M. ehrenbergii* of Europe, and I must hereby cancel the species established by me in 1896. The Illinois specimens range from 1½ mm. to 6 mm. in length, while the Michigan specimens measured only from 2 to 3 mm. In all of the small Illinois specimens the cephalic tracts of rhabditi are lacking, and are prominent only in the largest individuals. The largest of the specimens, 6 mm. in length, contained eight young worms in the left uterus, the right uterus being empty.

The viviparity of *M. ehrenbergii* was known to Focke (1836), and the same author has described the differences between the brown hard-shelled winter eggs and the smaller translucent summer eggs, and pointed out the fact that in the viviparous condition the young ones arise from the thin-shelled summer eggs. The simultaneous occurrence of both summer and winter eggs in the same individual was observed by Leuckart (1852). Four of the Illinois specimens contained the characteristic large opaque brown hard-shelled winter eggs, and therefore agree with the European form in producing both kinds of eggs at the same season, though in no case were there both kinds of eggs actually present in the same individual. About 40% of the individuals contained the translucent summer eggs, the smaller specimens showing no signs of sexual organs. The winter eggs have the same shape as those of the European species, such as would result if one half of a hollow sphere were infolded into the other half. As in the European species, too, the diameter of the winter eggs considerably exceeds that of the summer eggs, the former measuring 0.525 and the latter 0.350 mm. in diameter. The occurrence of *M. ehrenbergii* in the United States also gives to this well known species a cosmopolitan distribution.

Stenostoma leucops O. Schmidt.

Stenostoma leucops O. Schmidt, 1848, p. 59; Silliman, 1885, p. 55; Ott, 1892.
Stenostoma neoboracense Girard, 1893, p. 220.

Said to have been abundant in the aquaria of the laboratory during May, 1896. Of this species I received only some stained mounted specimens. The following account is from notes made by Dr. Kofoid upon living material.

When extended, in motion, the worms measured 1 to 1½ mm. in length. Margins transparent, central portion brownish, posterior third of the animal often with a faint tinge of pink or maroon, and in one specimen this color extended throughout the length of the animal. Several lobe-like projections on the surface near the mouth when the animal is contracted. The anterior end, when extended, exhibits two lateral depressions, — the ciliated pits. The projecting anterior end is very mobile, and from its activity undoubtedly highly sensitive. No trace of sexual organs. Cilia very prominent on the general surface of the body, and always directed forward when the animal is quiescent. Locomotion is sometimes in a posterior direction, and is accompanied by waves of constriction progressing from in front backwards. Forward motion, however, is apparently due wholly to ciliary action. Reproduction by fission was indicated in some specimens by the existence of well marked constrictions at about one third the total length from the posterior end; the constriction involved both the hypodermis and the digestive tract.

LIST OF WORKS REFERRED TO IN THE TEXT.

Baer, K. E. von.

1827. Beiträge zur Kenntniss der niedern Thiere. Nova Acta Acad. Cæs. Leop. Car., Tom. XIII. Pars 2, pp. 523–762, Taf. XXVIII.–XXXIII. [VI. Ueber Planarien, pp. 690–730, Taf. XXXIII.]

Borelli, A.

1895. Viaggio del dott. Alfredo Borelli nella Republica Argentina e nel Paraguay. Planarie d'acqua dolce. Boll. Mus. Zool. e Anat. Comp. R. Univ. Torino, Vol. X. No. 202.

Carrière, J.

1382. Die Augen von Planaria polychroa Schmidt und Polycelis nigra Ehrb. Arch. mikr. Anat., Bd. XX. pp. 160–174, Taf. IX.

Diesing, K. M.

1850. Systema Helminthum. Vol. I. Vindobonæ.

Diesing, K. M.

1862. Revision der Turbellarien. Sitszungsb. Akad. Wiss. Wien, Bd. XLIV. Abth. 1, pp. 485–578: Bd. XLV. Abth. 1, pp. 191–318.

Dugès, A.

1828. Recherches sur l'organisation et les mœurs des Planariées. Ann. Sci. Nat., Tom. XV. pp. 139–183, Pl. 4, 5.

Dugès, A.

1830. Aperçu de quelques observations nouvelles sur les Planaries et plusieurs genres voisins. Ann. Sci. Nat., Tom. XXI. pp. 72–90, Pl. 2.

Duyne, J. van.

1896. Ueber Heteromorphose bei Planarien. Arch. ges. Physiol., Bd. LXIV. pp. 569–574, Taf. X.

Focke, G. W.

1836. Planaria Ehrenbergii. Ann. Wiener Mus., Bd. I. pp. 193–206, Taf. XVII.

Girard, C.

1851. Brief Account of the Fresh Water Planariæ of the United States. Proc. Bost. Soc. Nat. Hist., Vol. III. pp. 264, 265.

Girard, C.

1851ᵃ. Die Planarien und Nemertinen Nord-Amerika's. Nord-Amerik. Monatsbericht Natur- u. Heilk., Bd. II. pp. 1–5.

Girard, C.

1893. Recherches sur les Planariés et les Némertiens de l'Amérique du Nord. Ann. Sci. Nat., Zool., Tom. XV. pp. 145–310, Pl. 3–6.

Graff, L. von.
1882. Monographie der Turbellarien. I. Rhabdocœlen. Leipzig.

Grube, E.
1872. Beschreibung von Planarien des Baikalgebietes. Arch. Naturg., Jahrg. 38, Bd. I. pp. 273–292, Taf. XI., XII.

Hallez, P.
1890. Catalogue des Turbellariés (Rhadocœlides, Triclades et Polyclades) du Nord de la France, etc. Lille. Also in Rev. Biol. Nord de la France, Tom. II., IV., V., 1890–93.

Hallez, P.
1892. Morphogénie générale et affinités des Turbellariés. Lille.

Iijima, I.
1884. Untersuchungen über den Bau und die Entwicklungeshichte der Süsswasser Dendrocœlen (Tricladen). Zeitschr. wiss. Zool., Bd. XL. pp. 359–464, Taf. XX.–XXIII.

Iijima, I.
1887. Ueber einige Tricladen Europa's. Jour. Roy. Coll. Sci., Imp. Univ. Japan, Vol. I. pp. 337–358, Plate XXV.

Kennel, J. von.
1888. Untersuchungen an neuen Turbellarien. Zool. Jahrb., Abth. Anat. u. Ont., Bd. III. Heft 3, pp. 447–486, Taf. XVIII., XIX.

Lang, A.
1884. Die Polycladen. Fauna u. Flora d. Golfes v. Neapel, XI. Leipzig.

Leidy, J.
1848. Descriptions of Two New Species of Planaria. Proc. Acad. Nat. Sci Philad., Vol. III. pp. 251, 252.

Leidy, J.
1848ª. Descriptions of Two New Species of Planaria. Ann. Mag. Nat. Hist., Ser. 2, Vol. I. p. 78.

Leidy, J.
1852. Helminthological Contributions, No. 2. Proc. Acad. Nat. Sci. Philad., Vol. V. pp. 224–227.

Leidy, J.
1852ª. Helminthological Contributions, No. 3. Proc. Acad. Nat. Sci. Philad., Vol. V. pp. 239–244.

Leidy, J.
1852ᵇ. Corrections and Additions to former Papers on Helminthology. Proc. Acad. Nat. Sci. Philad., Vol. V. pp. 284–290.

Leidy, J.
1885. Planarians. The Museum, Vol. I. No. 4, pp. 49–52.

Leuckart, R.
1852. Mesostoma Ehrenbergii, anatomisch dargestellt. Arch. Naturg., Jahrg. 18, Bd. I. pp. 234–250, Taf. IX.

Leydig, F.

1864. Tafeln zur vergleichenden Anatomie. Tübingen.

Oersted, A. S.

1844. Entwurf einer systematischen Eintheilung und speciellen Beschreibung der Plattwürmer, etc. Copenhagen.

Ott, H. N.

1892. A Study of Stenostoma leucops O. Schm. Jour. Morph., Vol. VII. No. 3, pp. 263–304, Plates XIV.–XVII.

Schmidt, O.

1848. Die rhabdocœlen Strudelwürmer (Turbellaria rhadocœla) des süssen Wassers. Jena.

Schmidt, O.

1862. Untersuchungen über Turbellarien von Corfu und Cephalonia. Zeitschr. wiss. Zool., Bd. XI. pp. 1–30, Taf. I.–IV.

Silliman, W. A.

1885. Beobachtungen über den Süsswasserturbellarien Nordamerikas. Zeitschr. wiss. Zool., Bd. XLI. pp. 48–78, Taf. III., IV.

Stimpson, W.

1857. Prodromus descriptionis animalium evertebratorum quae in Expeditione ad Oceanum Pacificum, etc. Pars I. Turbellaria dendrocœla. Proc. Acad. Nat. Sci. Philad., Vol. IX. pp. 19–31.

Weltner, W.

1887. Dendrocœlum punctatum Pallas bei Berlin. Sitzungsb. k. Preuss. Akad. Wiss., Bd. XXXVIII. pp. 795–804, Taf. VI.

Wheeler, W. M.

1894. Syncœlidium pellucidum, a New Marine Triclad. Jour. Morph., Vol. IX. pp. 167–194.

Woodworth, W. McM.

1891. Contributions to the Morphology of the Turbellaria. I. On the Structure of Phagocata gracilis Leidy. Bull. Mus. Comp. Zoöl., Vol. XXI. No. 1, pp. 1–42.

Woodworth, W. McM.

1896. Preliminary Report on Collections of Turbellaria from Lake St. Clair and Charlevoix, Michigan. Bull. Mich. Fish Commission, No. 5, pp. 94, 95.

Woodworth, W. McM.

1896ª. Report on the Turbellaria collected by the Michigan State Fish Commission during the Summers of 1893 and 1894. Bull. Mus. Comp. Zoöl., Vol. XXIX. No. 6, pp. 239–243.

Woodworth, W. McM.

1896ᵇ. Notes on Turbellaria. American Naturalist, Vol. XXX. pp. 1046–1049.

EXPLANATION OF THE PLATE.

ABBREVIATIONS.

brs.	Copulatory bursa.	*ov'dt.*	Oviduct.
dt. ej.	Ductus ejaculatorius.	*pe.*	Penis.
gl. sh.	Shell gland.	*ut.*	Uterus.
gl. pr'st.	Prostate gland.	*va. df.*	Vas deferens.
go'po.	Gonopore.	*vag.*	Vagina.
mu. ret.	Retractor muscle.	*x.*	Vesiculæ seminales.

The lines adjacent to the Figures 1, 2, and 4–7 indicate the natural size of the object.

Fig. 1. Dendrocœlum lacteum. From life, × 4.

Fig. 2. Planaria maculata. From life, × 6.

Fig. 3. P. maculata. Head end, to show the occurrence of the light median streak. From life.

Fig. 4. Planaria dorotocephala, sp. nov. From life, × 7. The line at the left of the figure indicates the natural size of the colored part of the figure only.

Fig. 5. Planaria gonocephala. From life, × 5.

Fig. 6. Mesostoma ehrenbergii, showing young worms in the left uterus. From a specimen in clove oil, × 14.

Fig. 7. P. dorotocephala, sp. nov., to show intestinal tract. A reconstruction from a series of frontal sections, × 6.

Fig. 8. Planaria unionicola, sp. nov. From a drawing, apparently from life, accompanying the specimen.

Fig. 9. D lacteum. Head end, to show the adhesive organ. From an alcoholic specimen killed in corrosive sublimate, × 5.

Fig. 10. D. lacteum. Diagram of sexual organs, × 20.

Fig. 11. D. lacteum. Longitudinal section to show the sexual organs, × 50.

Fig. 12. D. lacteum. Transverse section through penis, × 40.

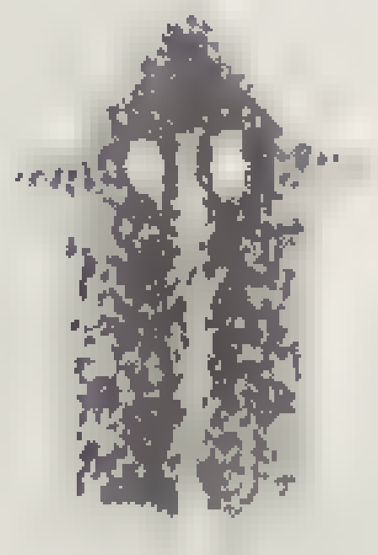
Fig. 13. D. lacteum. Transverse section through extreme anterior end, to show the adhesive organ, × 80.

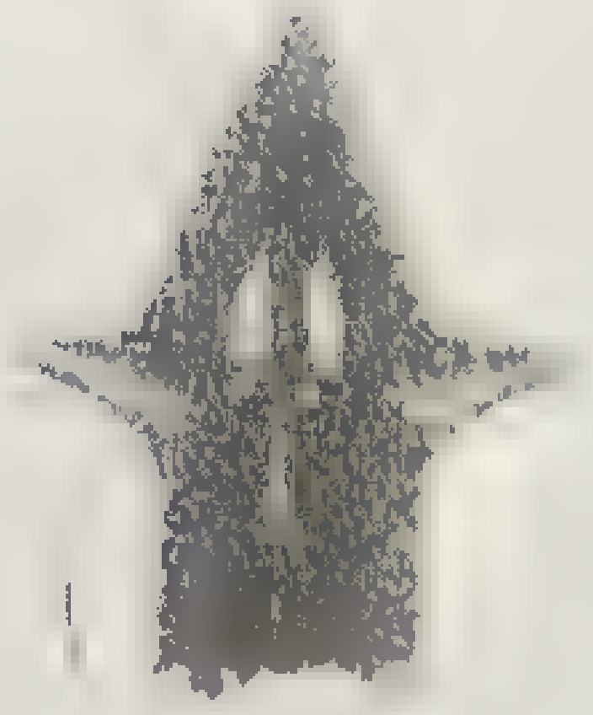
Fig. 14. D. lacteum. Transverse section from same individual as last, somewhat posterior to it, × 80.

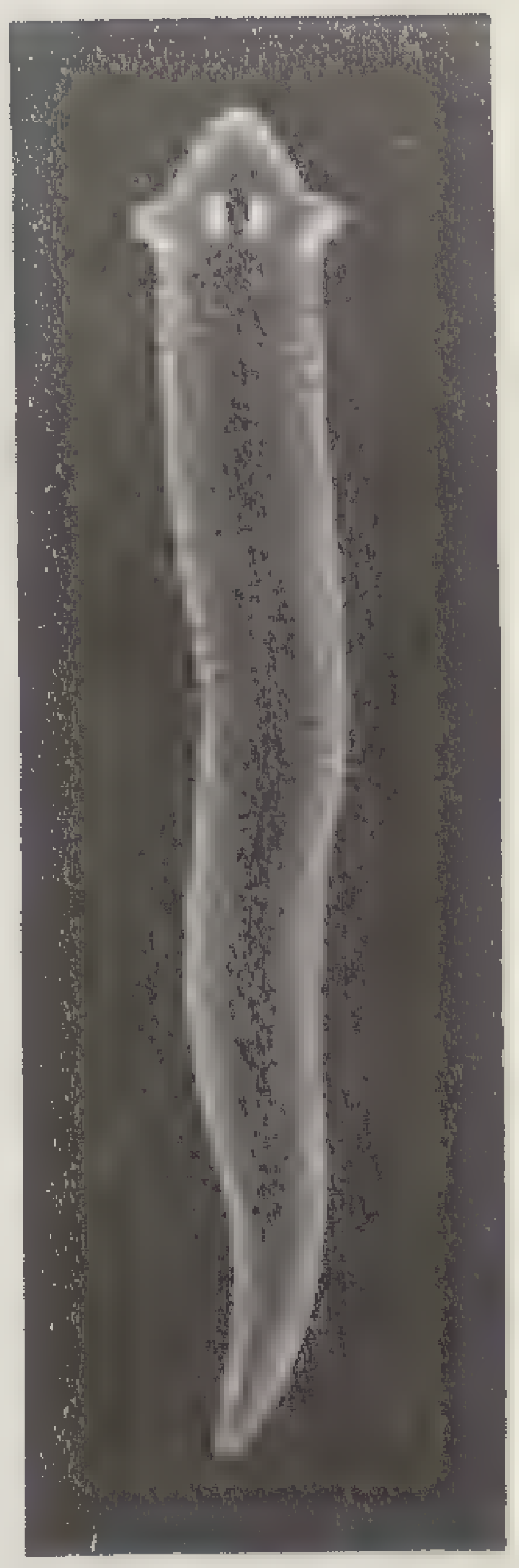
Fig. 15. D. lacteum. Median longitudinal section through the anterior end and adhesive organ, × 80.

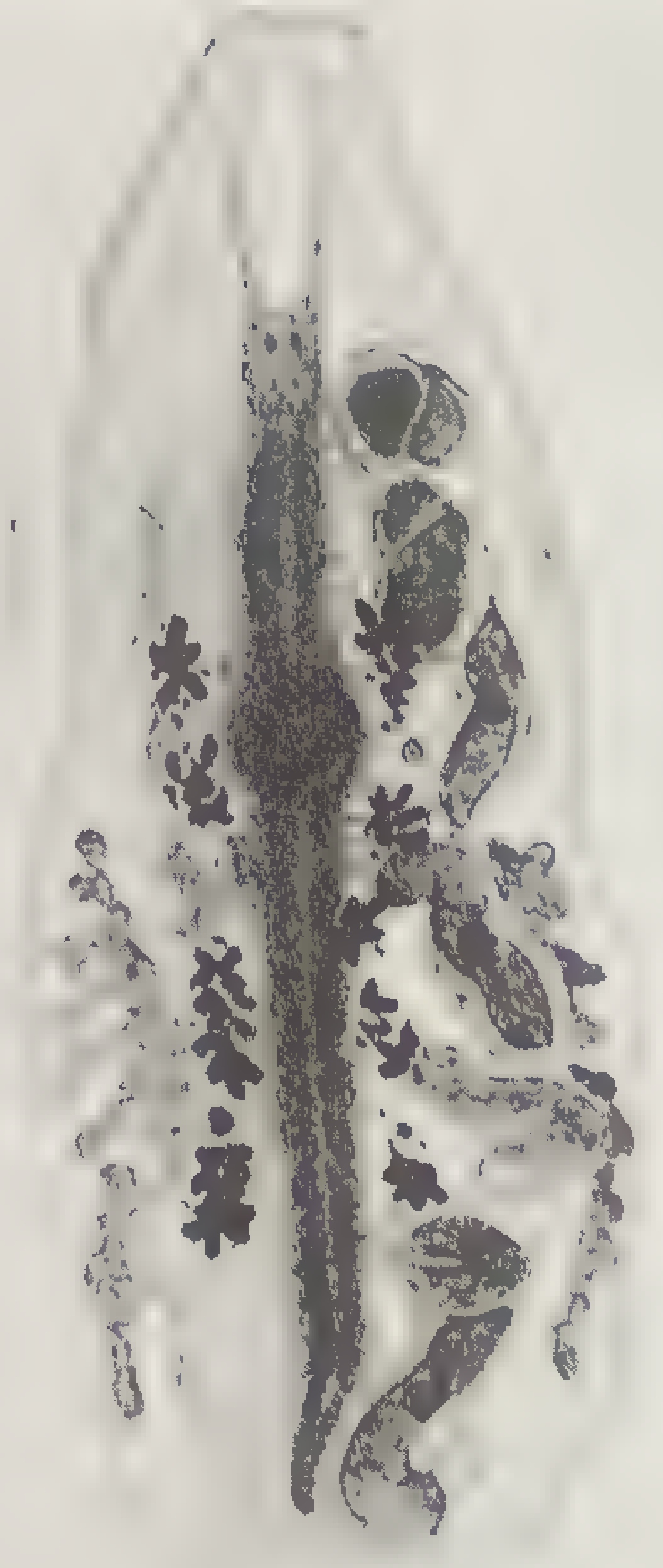
1.

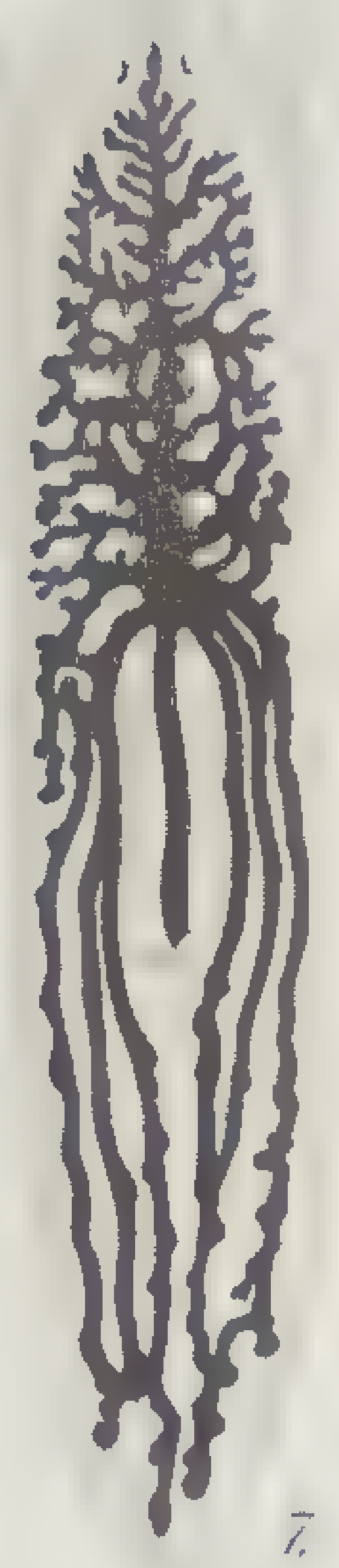
2.

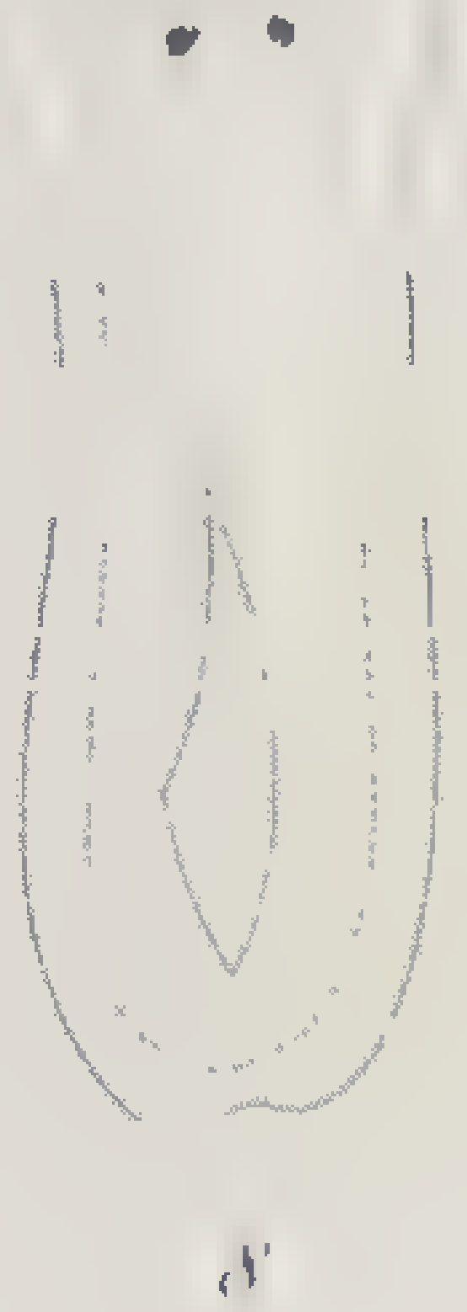

3.

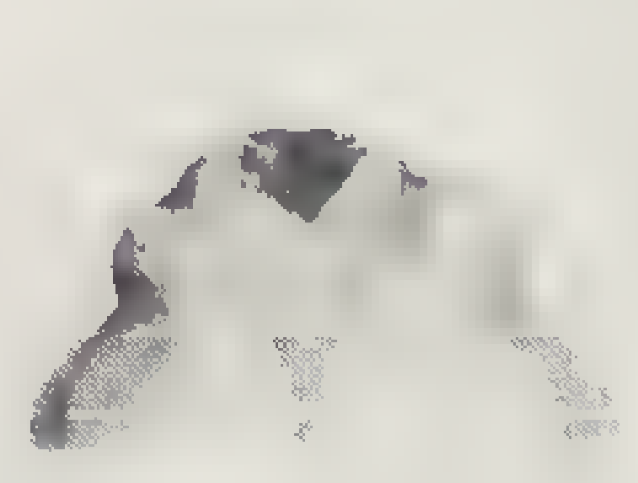

4.

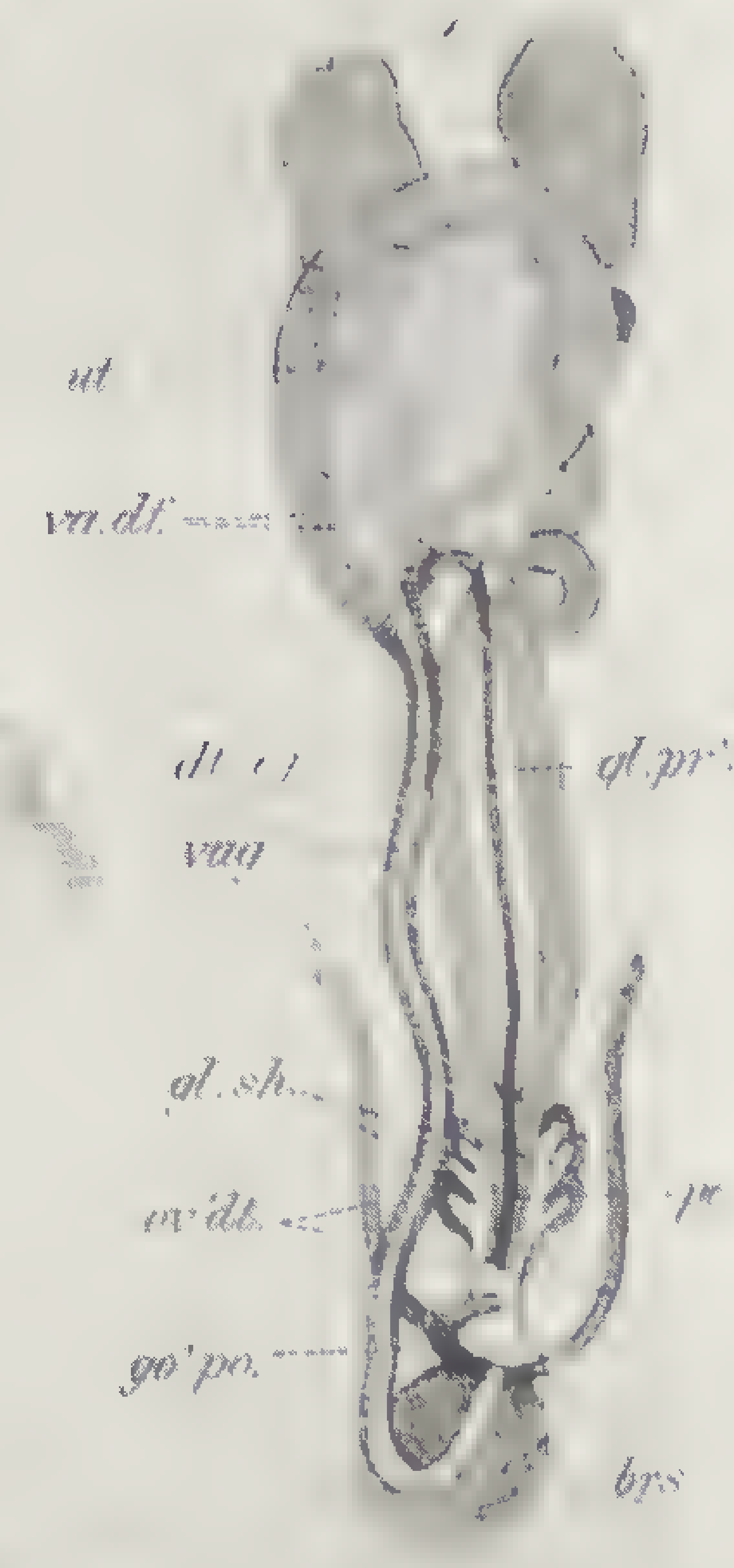

5.

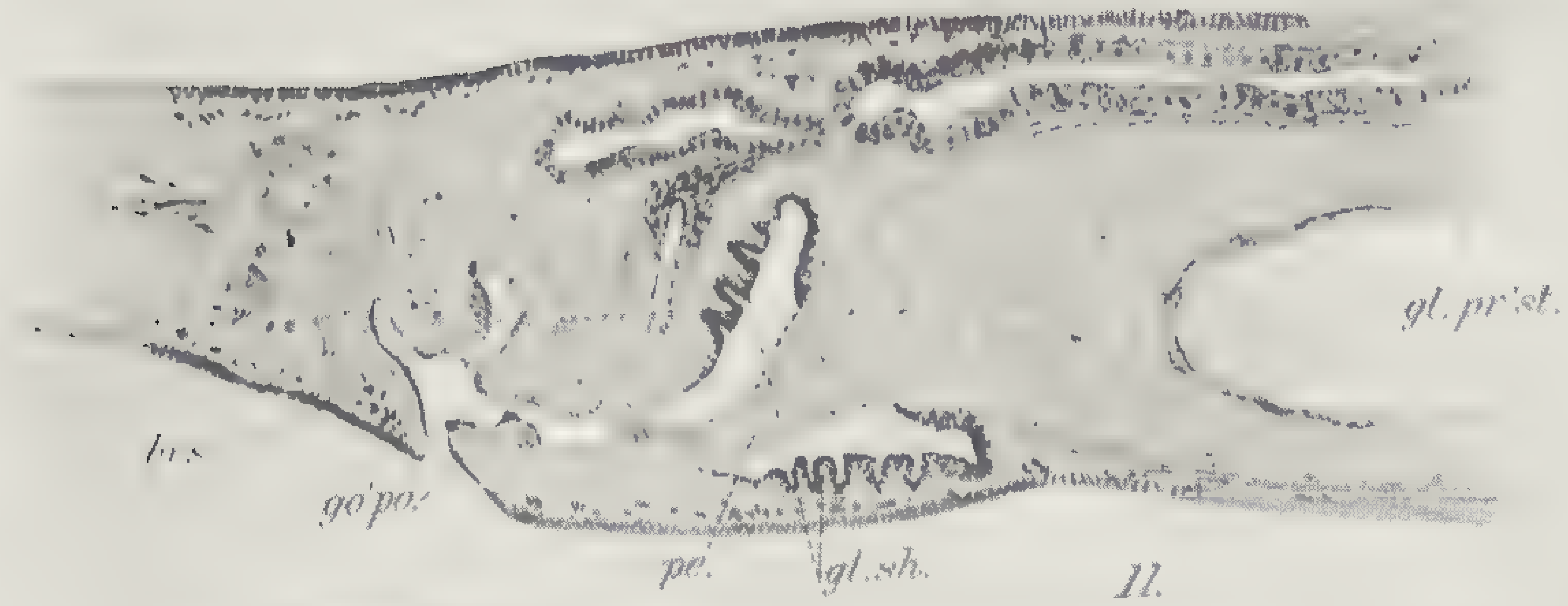

6.

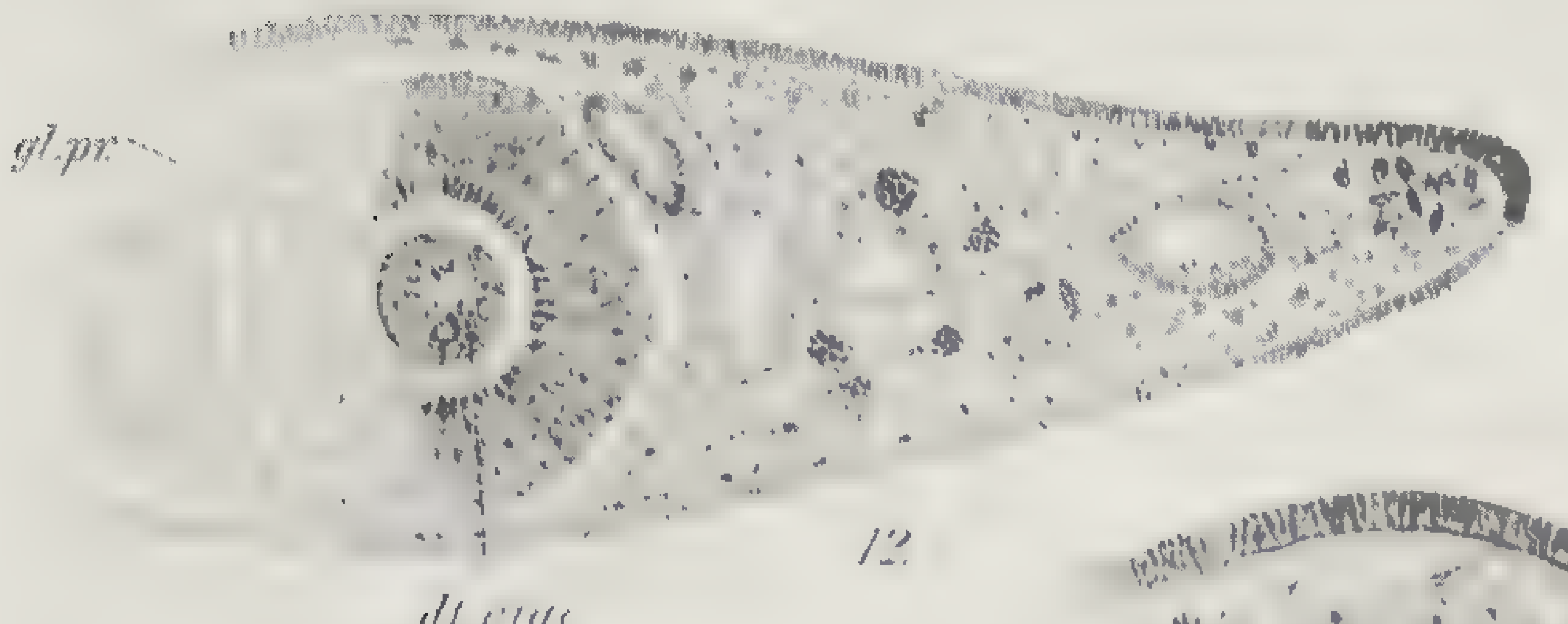

7.

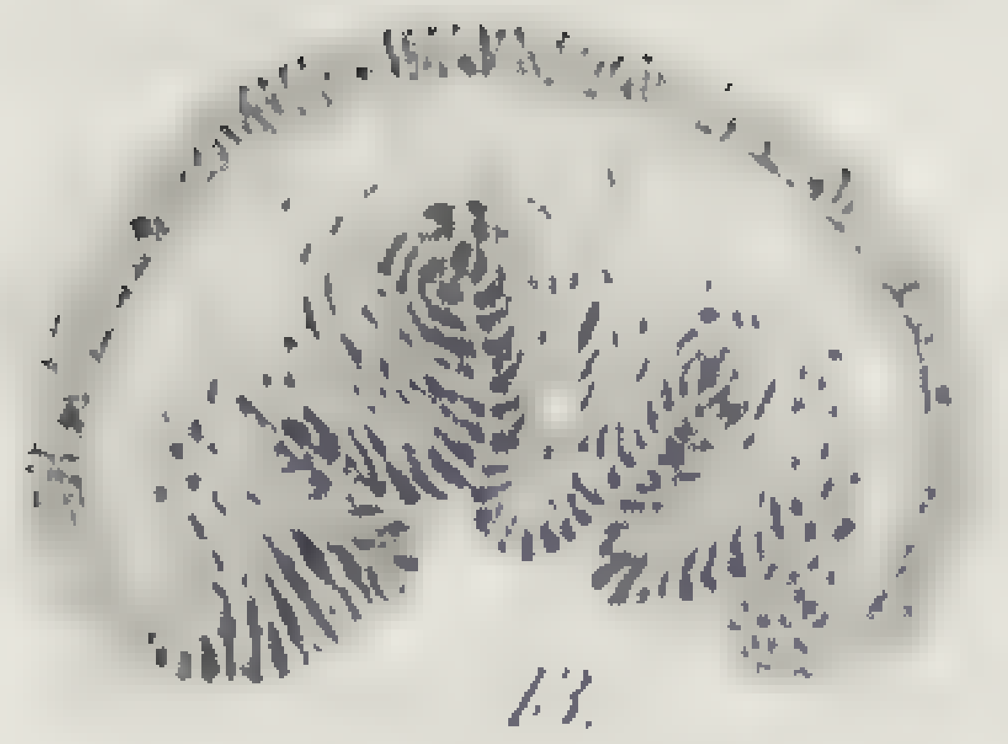

8.

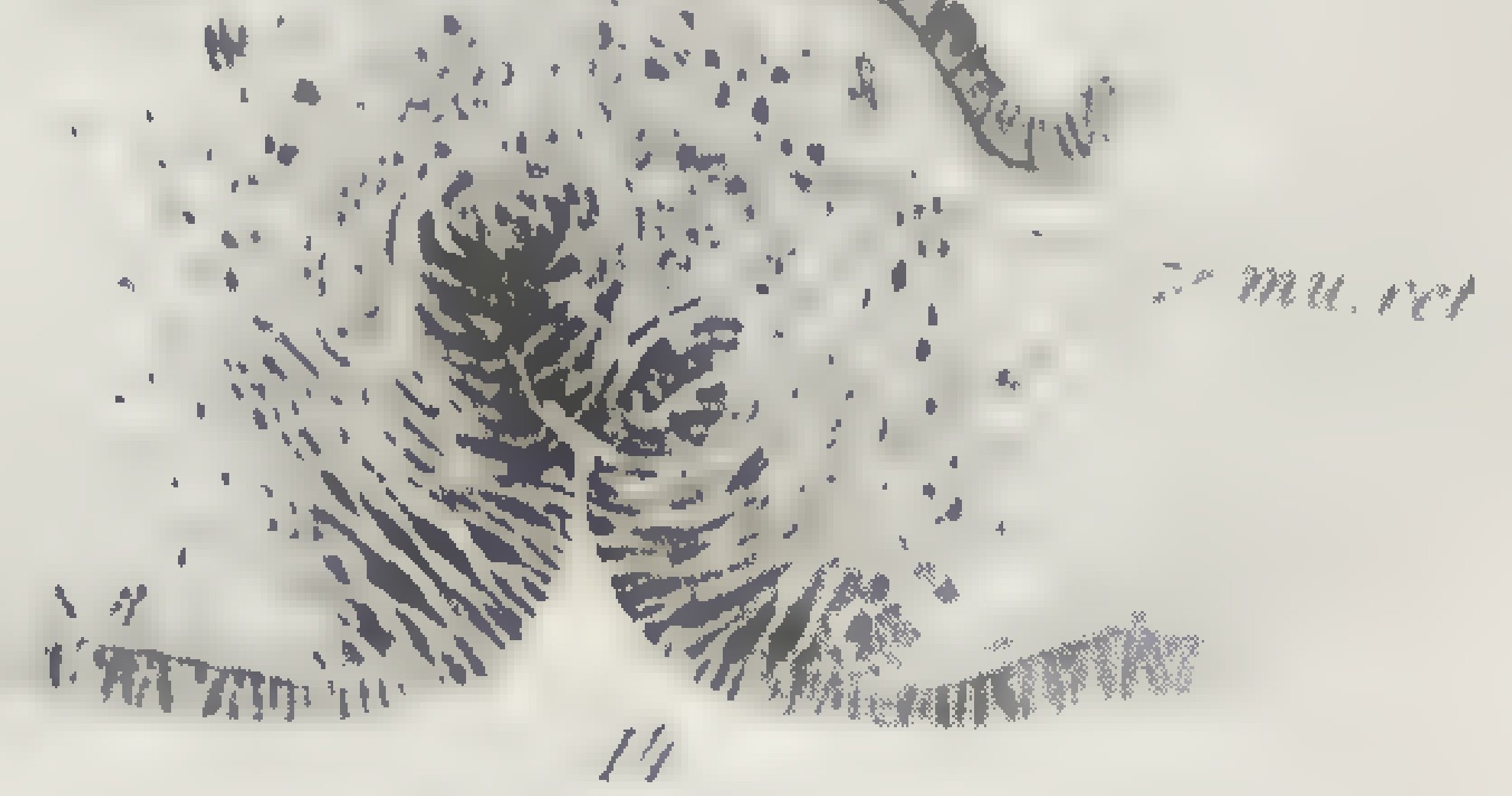

9.


ut
va.df.
dt.ej
gl.pr'st
vag
gl.sh.
ov'dt.
pe
go'po.
brs
10.

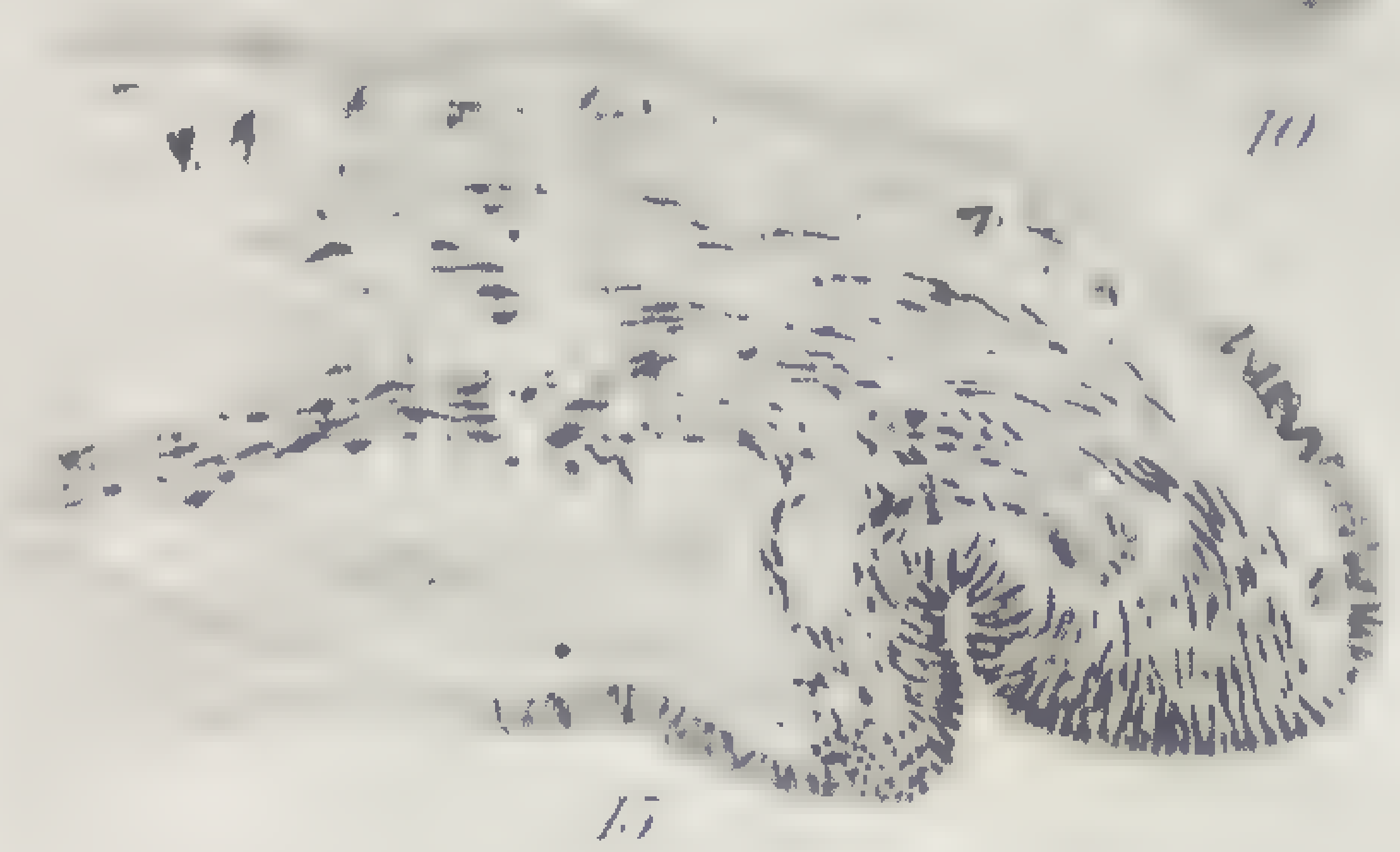

vag
gl.pr'st.
brs
go'po.
pe.
gl.sh.
11.


gl.pr.
dt.ejac
12.


13.



14.


15.

Heliotype Co. Boston

Bulletin of the Museum of Comparative Zoölogy
AT HARVARD COLLEGE.
Vol. XXXI. No. 2.

ON THE RELATIONS OF CERTAIN PLATES IN THE DINICHTHYIDS,

WITH DESCRIPTIONS OF NEW SPECIES.

By C. R. Eastman.

With Five Plates.

CAMBRIDGE, MASS., U. S. A.:
PRINTED FOR THE MUSEUM.
October, 1897.

No. 2. — *On the Relations of Certain Plates in the Dinichthyids, with Descriptions of New Species.* By C. R. Eastman.

The present contribution may be regarded as a continuation and enlargement of two previous articles on the Dinichthyids,[1] one of which discussed the relationships of certain detached and little known plates, and the other endeavored to trace the ancestry of the group. Some of the plates mentioned in the first paper are now illustrated and more fully described, together with others which afford additional evidence regarding the osteology of *Dinichthys;* and the views set forth in the second paper are now considered more in detail. In addition, descriptions are offered of several new species, and restorations are given of the dorsal and ventral aspects of *Dinichthys.*

Unless otherwise stated, the material upon which all of the following descriptions are based is preserved in the Museum of Comparative Zoölogy at Cambridge, Mass. To Mr. Alexander Agassiz, Director of the Museum, the most cordial and grateful thanks of the writer are due for the opportunity to study the collection, and to publish the results herein set forth.

Dorsal Plates. — It is proposed to consider first the system of plates covering the dorsal surface of the body in *Dinichthys.* These plates are shown in their natural arrangement, as known to exist in *D. intermedius* and *D. terrelli,* in Plate **1**, Fig. 1; their correspondence with homologous elements in *Coccosteus* and related genera will be obvious from an inspection of the diagrams. The restoration here given may seem to call for a word of explanation, since it differs in certain respects from the familiar ones of Newberry and others.[2] The cranial osteology is based upon one of the most perfect heads of *Dinichthys intermedius* ever discovered, now the property of the Cambridge Museum. A full description of the same specimen has already been published by E. W. Claypole.[1] Inasmuch as this cranium lacks the marginal and suborbital plates, these have been supplied in the diagram from Newberry's restoration. The fact that they are shown more in projection than perspective imparts a wider and more flattened appearance to the cranium than is strictly natural; the dorso-laterals are likewise drawn as if flattened out, instead of conforming to the curvature of the body. The outline of the dorso-median has been reduced to scale from a photograph of an exceptionally perfect plate obtained from Dr. William Clark by the British Museum; its exact position as regards the dorso-laterals has been ascertained from specimens in the Museum of Comparative Zoölogy. Hence the restoration can be considered as such only in the sense that the parts are now brought together in their completeness and proper relationships, and are shown on the same scale.

---

[1] Amer. Journ. Science, [4], Vol. II. pp. 46–50, July, 1896. Proc. Amer. Assoc. Adv. Science, Buffalo Meeting, August, 1896 (Abstract in Amer. Geol., Vol. XVIII. pp. 222, 223).

[2] Newberry, J. S., Palæozoic Fishes of North America (Monograph U. S. Geol. Survey, Vol. XVI. Plate LII. Fig. 2), 1889. Dean, B., Fishes, Living and Fossil, 1895, p. 134, Fig. 134.

The earlier restorations already referred to are subject to the following criticisms. First, the anterior portion of the dorso-median is produced in imagination so as to cover the exposed space behind the occipital region; secondly, the conditions of overlap and underlap are represented on only one side of the antero-dorso-lateral, instead of on three sides; thirdly, the postero-dorso-lateral is not shown at all.

Hitherto the postero-dorso-lateral has never been found in direct association with other plates, and its position has accordingly remained in doubt. It has long been known under Newberry's designation of "post-clavicular," and is a plate of not uncommon occurrence in the detached condition. Its triangular form, the markings impressed upon it by overlying plates, and the course of the sensory canal system across it, appeared to the writer[2] sufficient evidence for assigning the plate theoretically to the position indicated in the diagram; and it is therefore interesting to record the discovery of a specimen which establishes the entire correctness of this inference. The new specimen represents the right antero- and postero-dorso-lateral plates of *D. terrelli*, firmly articulated together, as shown in Plate 2, Fig. 1. It is from the Cleveland Shale, and was found in the vicinity of Lindale, Ohio, by Mr. Prentis Clark. The inner surface of the plates is alone visible, the external side being embedded in the matrix. The mode of articulation between the two plates is by pegs and sockets, the position of which is fairly constant among the specimens that have been observed. The largest and most perfect plate that the writer has seen is preserved in the Museum of Comparative Zoölogy, and measures 65 cm. in length (Catalogue No. 1325). The corresponding element in *D. intermedius* is hardly to be distinguished except for its smaller size. An excellent example of the latter species belonging to the School of Mines Cabinet of Columbia University shows the postero-dorso-laterals of either side of the body commingled with other plates pertaining to the same individual; it is valuable for furnishing comparative measurements of the different bones, and deserves further study.

---

[1] Claypole, E. W., The Head of Dinichthys (Amer. Geol., Vol. X. p. 199), October, 1892.

[2] Amer. Journ. Science, [4], Vol. II. p. 48, July, 1896.

The orientation of the plate in question may be readily determined, either by an inspection of the overlapped area, or by noting the course of the sensory canals. These arise at the anterior border, where they meet the single straight furrow that traverses the antero-dorsal-lateral; and from this point they sweep inwardly, sometimes as a single and sometimes as a double channel, as far as about the middle of the exposed portion of the plate, where they cease. In this respect the genus differs from *Coccosteus*, which has the canals continued on to, and in some cases entirely across, the dorso-median. The insunken area formed by the overlap of the latter plate stands in marked contrast to the irregular depressions produced by the overlap of the antero-dorso-lateral. The graceful curve forming the postero-lateral boundary of the dorso-median is projected upon the underlying plate, and shallow depressions are left where the transverse ridge on the under surface of the dorso-median rested on the subjacent plate. This ridge, it should be noted, occupies the same relative position as its homologue in *Coccosteus*.

The upper boundary of the lateral plates is indicated by a deeply insunken area on the antero-dorso-lateral, and a slight indentation on the free margin of the postero-dorso-lateral. Below, these as yet undiscovered plates must have been connected with the ventral armoring, either directly, or more probably through the intervention of the "claviculars." The curvature of the ascending arm of the latter furnishes us at the same time with the curvature of the missing laterals, and we can also form an approximate estimate of their height and length. It is to be hoped that the laterals may yet be identified as such, when the entire dermal covering of *Dinichthys* can be compared plate for plate with its European congeners.

Ventral Plates. — Grave difficulties have been encountered in the attempt to reconstruct the ventral armor of *Dinichthys*, owing to the detached condition in which the plates have invariably been found. It is perhaps but natural that the views which were originally entertained regarding the structure of the plastron should have received important modifications in consequence of later discoveries. Thus, Newberry's supposed posterior ventrals were afterwards identified as the suborbitals, and his so called "jugulars" have since been demonstrated by Wright[1] to be in reality the posterior ventrals.

The restorations of Wright and Dean[2] (the latter being somewhat modified after Wright's figures) leave the median plate or plates unaccounted for, and it remained for Dean in a subsequent publication[3] to reconstruct the ventral covering afresh, with the addition of a single element along the median line. But as pointed out by the present writer in a review of Dean's article,[4] the evidence is not entirely conclusive that a distinct antero-median ventral was not present in advance of the posterior element and overlying it, although now obscured on the specimen by weathering. The writer has since had an opportunity for examining the original, which is referred by Dr. Dean with some hesitation to *Dinichthys gouldi*. Although it is badly fractured precisely at the spot where we should expect a suture to exist, and therefore incapable of affording positive proof on this point, nevertheless the fact that the two plates we know were at least potentially present should have retained their normal position with respect to each other, while the adjacent plates have become displaced, points strongly toward a union of some kind between them.

For an undoubted example of fusion of the mid-ventrals we must turn to the specimen of *Dinichthys terrelli* figured by Newberry on Chart VI. (Figure A), accompanying the second volume of the Ohio Geological Survey Report. The original is still preserved in the School of Mines Cabinet, and has been recently refigured by Dr. Dean.[5] The resemblance of the anterior and posterior portions to plates presently to be described, and occurring as distinct elements, is sufficiently obvious. In this specimen, and the statement doubtless applies to all adult individuals of the same species, fusion exists between the mid-ventrals; in *D. gouldi* fusion probably likewise exists. These two instances are sufficient, in Dr. Dean's estimation, to compel us "to accept the thesis that the median ventral plates of *Dinichthys* must be separate or fused in *all* members of the genus."

---

[1] Wright, A. A., The Ventral Armor of Dinichthys (Amer. Geol., Vol. XIV. pp. 313–320), 1894. Report Ohio Geol. Survey, Vol. VII. pp. 620–626, 1893.

[2] Dean, B., Fishes, Living and Fossil, 1895, Fig. 135, p. 134.

[3] Dean, B., The Ventral Armoring of Dinichthys, etc. (Trans. N. Y. Acad. Sci., Vol. XV. pp. 157–163, May, 1896).

[4] Amer. Geol., Vol. XVIII. pp. 316, 317, 1896.

[5] Dean, B., Trans. N. Y. Acad. Sci., Vol. XVI. Plate III., 1897.

Under ordinary circumstances, such an interpretation would appear most logical, since we should expect, *a priori*, marked differences in the mode of union of the mid-ventrals to be indicative of different genera. We might reasonably infer that these differences were accompanied by variations in the dentition and other parts of the body, although this is a point which could only be determined empirically. Should it be ascertained, however, that forms existed having a like dentition, a like configuration and arrangement of plates as in *Dinichthys*, yet differing among themselves as respects the mode in which the median ventrals were united, there would be difficulty in estimating the value of this latter character. Ought it to be regarded as a valid generic distinction, or, other things being equal, merely as an adaptive variation affecting different species indiscriminately? From present indications it would appear highly probable that diverse conditions existed in the ventral plates of forms which agree in their remaining characters, so far as known, with *Dinichthys*. It must be noted, also, that amongst the species of this genus the paired ventral plates are exceedingly variable in their characters, more so in fact than any other plates of the body. Not only do they vary in form, relative proportions, and mode of union among different species, but there are considerable differences to be observed within one and the same species; one class of variations within specific limits will be referred to later under the head of ventro-lateral plates.

To sum up these difficulties briefly, we must admit on the one hand that theoretical considerations are opposed to the view that species of one and the same genus should differ widely as respects the number and arrangement of the median ventrals; but on the other hand, evidence is wanting to show that the forms they represent differed in any respects further than this from *Dinichthys*. And until positive evidence is forthcoming, such as finding the plates naturally associated with the dentition, it is impracticable to employ characters of the ventral plates as a test of generic rank. In our opinion, both prudence and convenience dictate that plates which resemble the known elements of *Dinichthys*, when found in the detached condition, are to be referred to that genus until criteria are at hand for determining them otherwise. Accordingly, certain isolated plates, whose description follows, will be referred to *Dinichthys* by virtue of their obvious affinities with that genus. And it will be assumed, provisionally at least, that in this genus the median ventrals may exist in three different conditions of union; they may simply overlap, as in *Coccosteus;* they may be fused into a single elongated piece; or they may be interlocked with one another. Examples of these three modes of union will now be considered.[1]

Interlocking Median Ventrals. — Two instances have been recorded where the median ventral plates of *Dinichthys* are articulated with one another; the first was made known by E. W. Claypole in 1893,[2] the second by the present writer in 1896.[3] In both cases the plates occurred in the detached condition, and were referred provisionally to the genus *Titanichthys.* Further investigation has since shown this to have been an erroneous determination, and the only genus that they can be certainly referred to in the present state of our knowledge is *Dinichthys.* The original of Professor Claypole's figure is preserved in the Museum of the Ohio State University at Columbus. It is a very large and heavy postero-ventro-median, and with it were associated the greater part of the postero-ventro-laterals. The proportions indicate a considerably larger species than either *D. terrelli* or *D. hertzeri,* and accordingly the name *D. ingens*[4] has been suggested for it by A. A. Wright. As a detailed description of these remains is in course of preparation by Professor Wright, it is sufficient for our purpose merely to cite this as an illustration of a particular mode of union between the median ventrals.

The other example of articulation or dovetailing is furnished by a specimen in the Museum of Comparative Zoölogy, now figured for the first time (Plate 2, Fig. 2). It is broadly lozenge-shaped, and its diagonals measure 20 by 31 cm. The resemblance of this plate to the posterior part of the single element in *D. terrelli,* already referred to, as figured by Newberry and Dean, is obvious. Its size, thickness, and markings impressed upon it by the paired ventrals, are also in substantial agreement. In these particulars it is seen to be closely allied to *D. terrelli;* but on the other hand the articulation with the antero-ventro-median is precisely the same as in *D. ingens.* The plate in question was collected by Mr. Terrell, in the Cleveland Shale of Lorain County, Ohio; but whether associated or not with other remains cannot now be ascertained. Theoretical considerations are certainly opposed to the idea that this plate pertained to either *D. terrelli* or *D. ingens;* and we are compelled to regard it as indicating an as yet unknown Dinichthyid species.

---

[1] See abstract of a preliminary paper by A. A. Wright, entitled, "New Evidence upon the Structure of Dinichthys" (5th Ann. Rep. Ohio State Acad. Sci., 1897, pp. 59, 60).

[2] Report Geol. Survey of Ohio, Vol. VII. p. 611, Plate XL. Fig. 1.

[3] Amer. Journ. Science, [4], Vol. II. p. 47.

[4] Should an identity be established between these plates and the mandible described by Claypole as *D. kepleri,* the latter name is entitled to priority.

Fused Median Ventrals. — Under this head must be placed the two examples already referred to, that have been described by Newberry[1] and Dean.[2] The originals are preserved in the School of Mines Cabinet at Columbia University, and have been determined as *D. terrelli* and *D.* (?) *gouldi.* Whether fusion took place as a strictly adaptive character in forms having a thin plastron, whether it occurred only in adult individuals, or whether it characterized all the individuals belonging to particular species, are questions for future discoveries to determine. That fusion did not exist in all species of *Dinichthys* appears, however, extremely probable.

Overlapping Median Ventrals. — Species which have the postero-ventro-median overlapped by the anterior element represent the normal or primitive condition, as exemplified by the genus *Coccosteus.* Three specimens of the detached antero-ventro-median and two of the postero-ventro-median are preserved in the Cambridge collection, whose relations to contiguous plates were plainly those of overlap and underlap. The bone shown in Plate 2, Figs. 5, 6, exhibits such a striking resemblance to its homologue in *D. terrelli,* that there can be no doubt as to its identity. It is evident that the plate under discussion is entire, since its margins taper gradually to a thin edge, and show no signs of having been broken away from a lower portion. Hence, the only important difference that is to be observed between this specimen and *D. terrelli* relates to the mode of union with the posterior element; in the present case it overlaps, in *D. terrelli* it is fused with the hinder piece. As we know of no other species to which it can be referred, we must include it, provisionally at least, under the last named species.

The special characters of this plate have been described elsewhere, although at that time the specimen was supposed to belong to *Titanichthys.* It may be remarked in passing that the semicircular flange forming the anterior margin (seen best on the ventral aspect) is continuous with similar compressed borders on the antero-ventro-laterals. None of these margins reveal any trace of plates overlapping them in front; so that an interlateral element, such as is present in *Coccosteus*, cannot be said to exist. We are therefore limited to assigning a strictly lateral (external) position for the so called "claviculars" or coracoids.

---

[1] Report Geol. Survey of Ohio, Vol. II. Part. II. (Palæontology), pp. 10, 31, and Chart VI. Fig. A.

[2] Trans. N. Y. Acad. Science, Vol. XV. pp. 157–163, 1896; Ibid., Vol. XVI. pp. 57–60, 1897.

A second specimen of the ventro-median preserved in the Cambridge collection (Catalogue No. 1299) shows the longitudinal ridge on the visceral surface more strongly developed than the first, and is both thicker and wider towards its posterior extremity.

There is yet a third specimen, which is smaller and of somewhat different configuration from the preceding; this is shown in Plate 3, Fig. 1. The visceral surface is embedded in the matrix, so that its character cannot be made out. In form it is somewhat suggestive of the parasphenoid bone of *Ctenodus*, but its structure as seen under the lens proves it to be Dinichthyid. The plate was obtained by Dr. Clark in the Cleveland Shale, near Lindale, Ohio. Owing to its smaller size, it may be referred with some reservation to *D. intermedius.*

From the same locality as the preceding, Dr. Clark has also obtained two unique plates, one of which is preserved in counterpart, and is shown in Plate 5, Fig. 1. Lanceolate in outline, and perfectly symmetrical, it presents a very graceful appearance; its length is 29 cm., and its maximum width 12.5 cm. Only the visceral aspect is exposed, and this is marked by two slightly oblique ridges, such as occur also in the corresponding position of *D. terrelli.* The plate is abruptly truncated in front, and bears indications of overlap by the antero-ventromedian. We shall find that additional light is thrown upon these relationships when we consider the plastron immediately to be described. The specimen is somewhat thinner than other ventral plates that have been noticed thus far, and it differs also in form. For the present, it must be regarded as representing an unknown Dinichthyid.

OVERLAPPING MEDIAN VENTRALS PRESERVED IN SITU.

So far, but two instances have been reported where the ventral plates were retained in their natural relations with respect to one another. The less perfect of these was described very briefly by von Koenen,[1] by whom it is doubtfully referred to *D. minor.* Only the left half of the plastron is preserved in this case; its entire length is assumed to have been about 16 cm., and its width 6 or 7 cm. The condition of the specimen is too imperfect to admit of a precise determination of the several elements, as the author has informed us by letter.

---

[1] Koenen, A. von, Ueber einige Fischreste, etc. (Abhandl. Gesellsch. Wissen. Göttingen, Vol. XL. p. 18), 1895.

The only other instance recorded where the plastron has been preserved *in situ*, is that made known by the writer at the Buffalo Meeting of the American Association for the Advancement of Science. For the discovery of this interesting fossil, science is indebted to Mr. F. K. Mixer, Curator of the Buffalo Society of Natural Sciences, who found the slab in place at the bottom of a small stream bed near Sturgeon Point, on the lake shore, twenty miles west of Buffalo, N. Y. The horizon at this point is the black Portage Shale, which has already yielded a considerable number of fish remains.[1] The plates were correctly determined by Mr. Mixer to be of Dinichthyid nature, and were so labelled by him and placed on exhibition in the Museum of the Buffalo Society. To this enthusiastic collector the writer is greatly indebted for the privilege of studying the specimen, and of presenting the following description of it.

Although the fossil has suffered considerably from aqueous and atmospheric erosion, the salient features have been so far preserved as to furnish points of control sufficient for reconstructing almost the entire topography. The slight extent to which the diagram given in Plate **1** has been reconstructed may be seen from a comparison with a photograph of the actual fossil, reproduced in Plate **4**. In most cases the sutural indications are so distinct, and continuous over such an area, that we have only to produce them in the same general direction across breaks in the surface until they meet, in order to complete the small portions that are interrupted. Thus, among the prominent landmarks that are left may be mentioned the terminal angles of the antero-ventro-laterals, which overlie the postero-ventro-laterals in their natural position. Half way between these points gives us the median line of the body; and as all the plates are arranged symmetrically with reference to it, it is clear that the fossil has been in no wise distorted. A knowledge of this fact permits us to supply the contours of one side from information derived from the other, and fortunately the two sides supplement each other to a remarkable degree. The only boundary lines that are not tolerably distinct are the forward portions of the antero-ventro-laterals. We will consider the relations of the different plates in order.

Ventro-Median Plates. — The first question that arises concerning the median ventrals is whether they are represented by one element or by two? And if two, what is their mode of union? We have no hesitation in answering that two median plates are present, and that the anterior overlaps the posterior, as in *Coccosteus.* The evidence appears perfectly decisive, and is of twofold nature; it depends upon a prominent surface elevation over the very region where we should expect the boundary between two median ventrals to be, and upon the fact that two centres of ossification are discernible.

---

[1] Mixer, F. K., Amer. Geol., Vol. XVIII. p. 223, October, 1896. Williams, H. U., Bull. Buffalo Soc. Nat. Sci., Vol. V. pp. 81–84, 1886.

The surface elevation referred to is palpably of the same nature as those prominences which are formed by the hinder extremities of the antero-ventro-laterals where they are superimposed upon the posterior pair of ventro-laterals. All of these elevations are more or less eroded in the specimen, but the one under consideration is scarcely more so than the others. If it were a purely fortuitous bulge of the surface, we should expect similar ones to occur elsewhere, whereas the prevailing aspect of the plates is flat and smooth. But inasmuch as the only remaining elevations are found at those places where we know for certain that boundaries occur, and as this occurs at the only place in the median line where we should expect to find a boundary, we are compelled to look upon this as a significant, not an accidental feature. Moreover, the shape of the elevation corresponds with the tapering extremity of the antero-ventro-median, superimposed upon the posterior element; and the outline of the latter is seen to be perfectly normal as compared with homologous plates, when we cut it off at this point. In fact, it is noteworthy that the shape of the postero-ventro-median bears a marked similarity to the bone last described (*supra,* p. 26), and shown in Plate 5, Fig. 1.

But still more pertinent evidence as to the existence of two median ventrals is furnished by the structure of the plates themselves. It is apparent at a glance that in the postero-ventro-median ossification proceeded from a single centre, which was nearly coincident with the centre of the plate itself. On holding the slab so as to reflect light at a proper angle, the course of vascular (Haversian) canals can be seen very distinctly, especially at the right anterior boundary; and all of these radiate toward the centre of the plate. Vascular canals are likewise apparent on the antero-ventro-laterals, but are only faintly perceptible on the antero-ventro-median. If the latter plate were articulated or fused with the posterior element, as in *D. terrelli,* it would be difficult to account for the significant elevation already referred to; and considering the relative thinness of the plates, such a mode of union could hardly have proved advantageous. It is more natural to suppose that the connection among all plates of the ventral armoring was one of simple overlap, as in *Coccosteus* and other forms.

Ventro-Lateral Plates. — The inner margins of the antero-ventro-laterals are traceable with certainty throughout the greater portion of their length, but with a lesser degree of probability for the remaining (anterior) portion, where they are not only much abraded, but in part covered over by extraneous fragments, as will be noted presently. The boundaries of these plates are more sinuous than in any other known species, and their proportions with respect to the posterior pair are also different. But, as already remarked, the ventrals exhibit a greater range of variation, even within specific limits, than all the other plates of the body.

One class of variations that deserves notice here is the relative length of the two sets of ventro-laterals. Sometimes the anterior pair is the longer, and again, apparently within the limits of the same species, the posterior pair exceeds them in length.

Possibly these differences may have been correlated with sex, a greater portion of the abdomen having been protected in the one case than in the other;[1] but however this may be, we are obliged to recognize the existence of these two patterns or varieties of the plastron. The present specimen, therefore, belongs to that type of plastron which has the anterior ventro-laterals longer than the posterior.

The external margin of the postero-ventro-laterals appears to have been evenly rounded. Unfortunately, the central portion of the plates has been eroded away, so that the contour of the inner margins can only be postulated. It is probable, however, owing to the tenuity of these plates, that the condition of their union was one of simple overlap; hence Dean's figures of *D. gouldi* (?) have been followed in restoring their inner boundaries. Of the anterior borders of these plates, no trace whatever remains. There may be some significance attached to the fact that the antero-ventro-laterals are symmetrically worn away, their present eroded margins forming a regular curve from the ventro-median outward. Whether this symmetrical wearing away was in any respect influenced by the anterior margins of the hinder pair of plates may perhaps be questioned; but at all events we must conclude that the former anterior boundary of these plates was not far from, and was probably parallel with, the interrupted edges of the antero-ventro-laterals. That the plates in question were separated for a considerable distance posteriorly, is witnessed by an impression of the visceral surface of the ventro-median, which is preserved as far as its posterior apex on the slab.

---

[1] Amer. Geol., Vol. XVIII. p. 317.

We have now to determine what species of *Dinichthys* is represented by the ventral armor just described. In the absence of the dentition, we must either associate the remains theoretically with mandibles of corresponding size that occur in the same horizon, or must regard the plastron as belonging to a new species. Fortunately, the proportions between the different body plates are well known in *D. terrelli* and *D. intermedius*, and from them we can readily compute the length of mandible and size of dorsal shield to which the present specimen would correspond. Thus, the ratio between the length of mandible and length of the antero-ventro-laterals in *D. terrelli*[1] is 1.14, and, assuming that about the same proportion held true for the species now under discussion, we should attribute it with a mandible 24 or 25 cm. long. Now, from the Genesee Shales near Bristol Center, New York, J. M. Clarke has described under the title of *D. newberryi* a mandible measuring 28⅓ cm. in length.[2] In the same horizon are also found detached dorsal shields which are considered by this writer as belonging to *D. newberryi*, although their dimensions correspond almost precisely with those of *D. minor*. In fact, Dr. Clarke's tables (pp. 22, 23) show that, while the mandibles of *D. newberryi* are about one half as large as in *D. hertzeri* and *D. terrelli*, the dorsal shields are less than one fifth the size of those in either species. Such a marked discrepancy of ratio appears incredible in the light of comparison with other species; and the measurements of the plastron now under discussion militate with the assumption that they, the mandibles of *D. newberryi*, and the dorsal shields from the same horizon as the last, all belonged to a single species. The correspondence of parts is such as to permit of a theoretical association of the plastron with the mandibles of *D. newberryi*, but not with the dorsal shields that are referred by Dr. Clarke to this species; these latter being more properly assignable to *D. minor*, or a species of equal size with *D. minor*.

It must be borne in mind, however, that these conclusions depend entirely upon empirical formulas; they are therefore more or less tentative and provisional. It may be presumed from the general nature of things, and in the absence of any contrary evidence, that the proportions existing between parts of the derm skeleton were fairly constant within the limits of one and the same genus. But the correspondence of parts as known in *Dinichthys* does not hold true by any means for other genera (*Trachosteus, Mylostoma,* etc.) belonging to the same family; and this fact admonishes us not to press hypothetical correlations too far, even within specific limits. Caution is enjoined in this particular case by yet another consideration. From the same locality and formation, Mr. Mixer has obtained a pair of mandibles associated with fragmentary Dinichthyid plates. The condition of these remains does not warrant a precise specific determination, but their affinities are probably with *D. minor.* The length of each ramus is about 17 cm., and the maximum height 5 cm. Either, therefore, these remains and the plastron represent together but a single species (*D.* ? *minor*), or we have evidence of two medium-sized species (*D.* ? *minor* and *D.* ? *newberryi*) in the Portage Shale.

---

[1] Wright, A. A., Report Geol. Surv. Ohio, Vol. VII. p. 626.

[2] Clarke, J. M., Bull. U. S. Geol. Survey, No. 16, p. 17, 1885.

Under these circumstances it is apparent that a positive identification of the species is impossible. For the sake of convenience, we might follow Dr. Clarke's example, and refer all the detached plates occurring in the Genesee Shales to *D. newberryi,* and all those from Portage Shale to *D. minor.* But there is no reason for supposing that each of these horizons contains but a solitary species; the indications point rather to the presence of more than one species in both horizons. And there is no reason why the doctrine of correlation of parts should not be applied to all the species of *Dinichthys* until experience has shown it to be invalid for some of them. Provisionally, therefore, we are in favor of referring the Portage plastron to the species with which it most closely agrees in measurement and geological horizon, that is to say, with *D. newberryi.* On the other hand, the Portage mandibles that have just been mentioned, and the detached dorso-median plates from the Genesee, may be referred provisionally to *D. minor.*

Comparative measurements of certain derm-plates for several species of *Dinichthys* are exhibited by the table on the following page.

Besides the plastron just described, there are several other interesting structures preserved on the same slab. In advance of the plastron are a number of badly weathered fragments, which evidently represent the dorsal plates of the body. The forward portions of both antero-ventrolaterals are covered over, and their proper boundaries obscured, by some of these fragments; but none of them are identifiable with certainty unless it be the antero-lateral tip of the dorso-median, which rests upon the angle of the right antero-ventro-lateral. This concealment of the underlying plates along their margins is unfortunate, since the restored anterior boundary has not such a clear basis of fact as one could wish

Comparative Measurements of Dinichthys Species.

No.	Species.	I. Length of Mandible.	II. Length of DM.	III. Length of DM without carinal process.	IV. Width of DM.	V. Length of A. V. L.	VI. Length of P. V. L.	VII. Length of Plastron.	VIII. Ratio between Columns II. and VII.
1	*D. ingens* . . .	. . .	. .	. .	. .	. .	76 +		
2	" *hertzeri* . . .	59.0	67.5	. .	53.0				
3	" *terrelli* . . .	56.25	65.0	36.0	57.5				
4	" " . . .	36.83	48.26	33.02	43.18	40.91	40.64	69.85	1.45
5	" " . . .	. . .	. .	. .	. .	48.26	55.88	90.17	1.87
6	" *newberryi* . .	28.33							
7	Portage plastron	. . .	. .	. .	. .	20.0	17.0	30 +	
8	*D. gouldi* . . .	17–20	. .	. .	. .	. .	12.6	8 +	
9	" *intermedius* .	22.86	41.91	29.21	26.67	17.15	22.86	35.56	0.85
10	" *minor* . . .	10 +	20.32	12.2	13.15	. .	. .	. .	1.59
11	Detached DM of Genesee Shale	. . .	. .	12.5	13.75				

for. At the same time it must be remembered that the front margin of the plastron in all species of *Dinichthys* conforms to a peculiar and well marked type.

To the right of the left antero-ventro-lateral is a small cleaver-shaped plate (7.5 cm. long by 3 cm. wide), the like of which is unknown among the derm plates of Coccosteids. It certainly does not belong to the dental apparatus, and is excluded from the orbital region on account of its size. There can be no doubt that the plate is entire, or nearly so; but we must confess ignorance as to its position on the body. Just behind the unidentified plate is to be seen a small portion of the vertebral axis, very imperfectly preserved, together with supports for the dorsal fin. The form of the neural arches is shown with some distinctness, as well as their articulation with the proximal row of basal cartilages. The outer tips of the distal row of basals appear to have been bluntly terminated, or even swollen.

Descriptions of New Species.

Under this heading are included, besides species altogether new to science, certain others which are now demonstrated for the first time to belong to the genus *Dinichthys*. The subject may be properly introduced by a consideration of the latter forms first.

As is well known, a large number of genera and species of Arthrodires have been founded on detached fragments, which commonly yield but little insight into the structure of the fish as a whole. Sometimes our knowledge of these forms is increased by the discovery of more perfect specimens, or by finding parts in natural association with the dentition or with other parts. The dentition obviously yields the most trenchant characters that can be employed for the discrimination of species; but in *Dinichthys* scarcely less important characters are furnished by the dorso-median plate. Owing to the massiveness of this plate, it is not readily subject to fracture or distortion, and is perhaps of more frequent occurrence than any other plate in the body. Its configuration varies markedly amongst the different species of *Dinichthys*, but remains fairly uniform within the limits of one and the same species; hence its systematic importance is very great.

There is one feature about the dorso-median which appears to be peculiar to the Dinichthyids; or, to put it differently, the Dinichthyids are distinguished from remaining Coccosteids by the possession of a certain characteristic structure; and this is the large, excavated carinal process by which the dorsal shield is terminated posteriorly. (See Plate **2**, Figs. 3, 4; Plate **3**, Figs. 2, 3.) All of the *Coccosteidæ*, so far as known, have a median longitudinal keel or ridge on the inferior surface of the dorso-median; but it is developed to a different degree, and is terminated in a different manner, amongst the several genera. In *Coccosteus* it ends posteriorly in a simple blunt spine; in *Homosteus* the ridge is stronger, and terminates in a knob at the posterior border of the shield; and in *Heterosteus* the keel is greatly developed, but is not produced behind the margin to any great extent, nor is it excavated superiorly. This series of Coccosteid genera leads up to the conditions that exist in the Dinichthyid group, where the inferior ridge is terminated posteriorly by a distinct process, such as is unknown in other members of the family. If we arrange the Dinichthyid forms in order of relative development of the carinal process, we shall have the following series: *Coccosteus* sp. Pander (hereinafter described as *D. livoni-*

cus); a form from the Eifel Devonian, described below as *D. pelmensis; Pelecyphorus* Trautschold; *Asterolepis bohemica* Barrande (hereinafter described as *D. bohemicus*); *Dinichthys;* and lastly, the genus *Titanichthys*, which is so closely allied to *Dinichthys* as to pass for a mutation or modification of the same. *Titanichthys* is, essentially, a huge *Dinichthys* with lighter bones and a degenerate dentition. It is presumable that when the osteology of *Brontichthys*, *Gorgonichthys*, *Mylostoma*, *Trachosteus*, and related genera, shall have become known as fully as in *Dinichthys*, their affinities with one another will be found to be much closer than with the more primitive Coccosteids. Newberry was inclined to regard these forms as constituting a distinct family, the *Dinichthyidæ;* but that would rather overreach the mark. We venture to adopt the middle course, and assign to the forms enumerated above the rank of a subfamily, known as the *Dinichthyinæ*.

As already remarked, we may regard the presence of a carinal process as sufficient ground for referring detached dorso-median plates to the *Dinichthyinæ*, instead of the *Coccosteidæ* in general. For precise generic determination, a knowledge of the dentition is of course necessary; but where we are in ignorance of the dentition, we may conveniently place all species founded upon such dorsal shields, for the time being at least, under the single genus *Dinichthys*. Precedent for this is already furnished by *D. precursor*, *D. ringuebergi*, *D. tuberculatus*, and the plates from the Genesee Shale referred to above as *D.* (?) *minor*. To this category may now be added the following new species: *D. livonicus*, *D. trautscholdi*, *D. pelmensis*, and *D. pustulosus*.

Dinichthys livonicus nomen nov.

1857. *Coccosteus* aus Livland, C. H. Pander, Ueber die Placodermen des devonischen Systems, p. 70, Plate B, Fig. 4.

1889. *Coccosteus*, H. Trautschold, Ueber Coccosteus megalopteryx, etc. (Zeitschr. deutsch. geol. Gesellsch., Vol. XLI. p. 38).

1896. *Dinichthys livonicus*, C. R. Eastman, Observations on the Dorsal Shields in the Dinichthyids (Amer. Geol., Vol. XVIII. p. 222).

The original of Pander's Plate B, Fig. 4, of his Placodermen des devonischen Systems, may be taken as the type of this species, and there may be presumably associated with it the specimen referred to by A. S. Woodward (Brit. Mus. Cat. No. P. 4731), in his Catalogue of Fossil Fishes, Vol. II. p. 293. Without doubt this represents one of the smallest and most primitive species of *Dinichthys*, yet its marked development of the carinal process in proportion to its size is sufficient reason for excluding it from *Coccosteus*. It apparently has much in common with the type of dorso-median described by Trautschold as *Pelecyphorus*, but may best be considered as representing a distinct species.

Formation and Locality. — Devonian; Livonia and Government of St. Petersburg.

Dinichthys trautscholdi nomen nov.

1889. *Coccosteus megalopteryx*, H. Trautschold, Ueber Coccosteus megalopteryx, etc. (Zeitschr. deutsch. geol. Gesellsch., Vol. XLI. pp. 38–45, Plate V. Figs. 1–6.)
1890. *Coccosteus megalopteryx*, O. Jaekel (Neues Jahrb., Vol. II. p. 145).
1890. *Pelecyphorus*, H. Trautschold (Zeitschr. deutsch. geol. Gesellsch., Vol. XLII. p. 576).
1891. *Pelecyphorus*, G. Gürich, Ueber Placodermen und andere Fischreste im Breslauer mineralogischen Museum (Zeitschr. deutsch. geol. Gesellsch., Vol. XLIII. p. 906).
1896. *Dinichthys trautscholdi*, C. R. Eastman, Observations on the Dorsal Shields in the Dinichthyids (Amer. Geol., Vol. XVIII. p. 222).

The type specimens represented in Plate V. Figs. 1–6 of Trautschold's paper on *Coccosteus megalopteryx* (*loc. cit.*, 1889), are now preserved in the Breslau Museum. They are from the Devonian of the River Ssjass, in Northwest Russia, and are apparently very closely related to the foregoing species. The principal differences consist in the larger size and less strongly arched condition of the dorso-median proper, and the different shape and position of the carinal process. The latter is more deeply excavated on its posterior face, stands nearly at right angles with the surface of the shield proper, and is given off from it slightly in advance of the hinder margin of the same. In this last respect we find a resemblance to the dorso-median described by Newberry as *D. precursor;* and, as in most American species, the process bears distinct traces on its inferior surface of the attachment of muscles (Trautschold, *loc. cit.*, Plate V. Fig. 6). On the other hand, *Coccosteus*-like affinities are shown by the tuberculated surface of the dorso-median, and by the presence upon it of sensory canals. These curve around toward one another posteriorly, but are not continued across the middle of the shield. The development of the inferior ridge and its terminal process is very pronounced. The dimensions of the largest process observed by Trautschold are stated to be 6.5 cm. in height by 3 cm. in width at the base, — proportions which are eminently Dinichthyid.

This species, which it seems proper to name in honor of its original describer, Professor Trautschold, was confused by this author with a Selachian ichthyodorulite which he mistook for a swimming appendage of *Coccosteus.* Later, when it was pointed out that *Coccosteus* could not properly include either of these forms, a new generic title was proposed for each, — *Megalopterix* for the ichthyodorulite (afterwards discovered to be identical with *Psammosteus*), and *Pelecyphorus* for the dorsal shields. Curiously enough, the species were left unnamed in both cases, except that provision was made for calling them both *Megalopterix securigera* in the event of their being proved to represent but a single species of one and the same genus. The generic title *Pelecyphorus* is preoccupied.

Formation and Locality. — Devonian; River Ssjass, Government of St. Petersburg.

Dinichthys pelmensis sp. nov.

Plate 2, Fig. 4.

The type of this species is represented by a specimen in the Schultze Collection belonging to the Museum of Comparative Zoölogy (Cat. No. 1375). It is from the Middle Devonian of Pelm, in the Eifel.

The greater portion of the left side of the dorso-median is preserved entire, but on the right side there remains only an impression of the under surface of the bone. The carinal process is admirably preserved, and is of large size in proportion to the dorsal shield proper. It is deeply hollowed out posteriorly, and stands less nearly perpendicular to the surface of the shield than in the two preceding species. The height of the process is 1.2 cm., and its maximum breadth 0.5 cm. The shield proper is 5.0 cm. long, and rather less than 4.5 cm. broad anteriorly. It is slightly arched transversely, and appears to have been emarginate in front. The sensory canals are distinctly traceable as far as the bone is preserved. That on the left side is seen to begin at a point about half way between the antero-posterior extremities of the shield, whence it continues nearly parallel with the postero-lateral margin of the same, but stops short of the median line shortly in advance of the process. Only the bare termination of the canal belonging to the right side is preserved on the present specimen. The surface of the plate is covered with fine reticulating ridges, at the intersections of which traces of minute tubercles are discernible. The effect of weathering, however, has been to reduce these, so that to the unaided eye the surface appears to be finely granulated. The thickness of the plate does not exceed 2 mm. except in the vicinity of the median longitudinal ridge.

Formation and Locality. — Middle Devonian; Eifel District.

Dinichthys eifeliensis Kayser.

Plate 3, Fig. 3; Plate 5, Fig. 4.

1880. *Dinichthys eifeliensis*, E. Kayser, Zeitschr. deutsch. geol. Gesellsch., Vol. XXXII. p. 817.

1895. *Dinichthys eifeliensis*, A. von Koenen, Ueber Fischreste des norddeutschen und böhmischen Devons (Abhandl. Ges. Wissensch. Göttingen, Vol. XL. pp. 16–18, Plate IV. Figs. 4, 5; Plate V. Fig. 1).

The mandibles of this species are estimated by von Koenen to have measured upwards of 50 cm. in length, and as it is the only Dinichthyid previously known with certainty from this locality, we may safely refer to it the specimens figured in the accompanying plates. That shown in Plate **3,** Fig. 3, represents without doubt the carinal process of a large dorsal shield, such as could well have belonged to a species as large as *D. eifeliensis.* Two or three additional specimens of the process, and several detached plates that are referable to the same species, also form a part of the Schultze Collection. One of these, identifiable as the right antero-ventro-lateral, is shown in Plate **5,** Fig. 4.

Formation and Locality. — Middle Devonian; Gerolstein, Berndorf, and elsewhere in the Eifel District.

Dinichthys bohemicus (Barrande).

Plate 2, Fig. 3; Plate 5, Fig. 2.

1872. *Asterolepis bohemica,* J. Barrande, Système Silurien de la Bohême, Vol. I. Suppl., p. 637, Plate XXIX. Figs. 9–13.

1880. *Asterolepis bohemica,* A. von Koenen, Abhandl. Ges. Wissensch. Göttingen, Vol. XXX. p. 4.

1895. *Anomalichthys bohemicus,* A. von Koenen, Abhandl. Ges. Wissensch. Göttingen, Vol. XL. pp. 8, 21.

There can be no difficulty in recognizing the form commonly known as *Asterolepis bohemica* Barr., since fossil fishes are not numerous in the Devonian of Bohemia, and this one is distinguished by its peculiar ornamentation. The tubercles are rather closely set, conical, and their summits, instead of being smooth, are finely punctate. The plates are of relatively large size, and usually exhibit considerable convexity.

There are two specimens of the dorso-median preserved in the Schary Collection, now the property of the Museum of Comparative Zoölogy, besides the impression of a third plate supposed to be one of the ventro-laterals. They are all from the same horizon, and two are from the identical locality as Barrande's type specimens. As has already been pointed out by von Koenen (*loc. cit.*, 1895, p. 8), it is extremely improbable that the figures given by Barrande are of the dorso-median. Their lack of bilateral symmetry, and their relative thinness, compel us to locate them elsewhere, perhaps on the ventral surface.

Certain it is, however, that the specimens shown in the accompanying figures represent the median dorsal plate. Not only do they fulfil the requisite conditions of shape, symmetry, and thickness, but both of them present fractures on the posterior end, where the carinal process has been broken off, leaving a cross-section of the inferior longitudinal ridge. On the strength of this evidence we are obliged to assign the species to *Dinichthys.* One of the plates has the inferior ridge much more strongly developed than the other, and differs considerably in form. But the ornamentation is essentially the same, and we are content to refer them both to *D. bohemicus*, since the coinage of new specific titles to include uncharacteristic fragments is greatly to be deprecated. Barrande's *Coccosteus fritschi*, as von Koenen has already surmised, is probably founded on the dorso-median of *Aspidichthys*.

Formation and Locality. — Middle Devonian (Étage Gg¹); Bohemia.

Dinichthys tuberculatus Newb.

1888. *Dinichthys tuberculatus*, J. S. Newberry, On the Fossil Fishes of the Erie Shale of Ohio (Trans. N. Y. Acad. Sci., Vol. VII. p. 179).

1889. *Dinichthys tuberculatus*, J. S. Newberry, Palæozoic Fishes of North America (Monogr. U. S. Geol. Surv., Vol. XVI. pp. 98, 99, Pl. XXXII. Fig. 3).

1889. *Dinichthys pustulosus* (*errore*), M. Lohest, De la découverte d'espèces américaines de poissons fossiles dans le Dévonien supérieur de Belgique (Bull. Soc. Géol. Belge, Vol. XVI. p. lvii).

1892. *Dinichthys pustulosus* (*errore*), [E. D. Cope], American Devonian Fishes found in Belgium (Amer. Naturalist, Vol. XXVI. p. 1025).

It is proper to record this species in connection with the foregoing, not only in order to complete the list of European representatives of the genus, so far as they have been described, but also because this is the only species of *Dinichthys* which is known to be common to both continents. This form may be regarded as the connecting link between the Old World species and the New; not that all the American Dinichthyids were derived from this species, but that this is one of the bonds through which the ancestry of the Western fishes can be traced backward to its starting point in Northern Europe. This chain of forms leads us eastward from Manitoba, through Iowa, Wisconsin, and Ohio, to New York and Pennsylvania; from the last named State *D. tuberculatus* carries us across the Atlantic to Belgium; next we meet with *D. eifeliensis* and *D. pelmensis* in Germany, followed by one species in Bohemia; and finally we come up with *D. trautscholdi* and *D. livonicus* associated with the ancestral *Coccosteus* and other derivatives from the same stock in the Devonian of Northwest Russia.

Formation and Locality. — Chemung Group; Pennsylvania. Psammite de Condroz; Belgium.

It remains only to present a description of certain Dinichthyid remains from the Hydraulic Limestone beds of Milwaukee, Wisconsin, a locality from which none have hitherto been known.

Dinichthys pustulosus sp. nov.

Plate 3, Fig. 4.

The F. H. Day Collection, purchased by the Museum of Comparative Zoölogy in 1881, contains a number of fish remains from the Hydraulic Cement Quarries near Milwaukee, Wisconsin. Among them are two plates whose preservation is such as to warrant description, especially since up to the present time but two species (*Rhynchodus greenei* and *Heteracanthus politus*) have been noticed from this locality.

The first of these (Plate 3, Fig. 4) is easily recognizable as the left antero-dorso-lateral of a new species of *Dinichthys*, and is chiefly remarkable for its finely tuberculated style of ornament. This plate is nearly twice the size of the corresponding element described by Newberry as *D. tuberculatus*, its articulating condyle is differently situated, and the tuberculation is entirely dissimilar. Of *D. tuberculatus*, Newberry [1] speaks as follows: "The tuberculation of the surface is relatively coarse, and the tubercles vary much in size and are irregularly scattered. Most of them seem to be hemispherical and plain, but others are more or less pitted, and a few are stellate." In the present species the tubercles are small and closely crowded, and are distinctly stellate at their bases.[2] It is somewhat surprising that there should be so few American species which present the characteristic surface ornamentation of the *Coccosteidæ;* the inference is that the tuberculated are more primitive than non-tuberculated forms.

A longitudinal fracture traverses the plate to the left of the sensory canal. It is interesting in that it displays very clearly the course of the vascular (Haversian) canals, which run essentially parallel with the surface of the plate. The canals are also well shown where the articulating condyle has broken off; and from their direction it would appear that the plate had grown by increments to the visceral surface only.

The second specimen in this collection that deserves notice is evidently the impression of one of the ventral plates, probably the left antero-ventro-lateral, the substance of the bone itself being entirely worn away. The surface ornament cannot be discovered from this specimen, but several fragments associated with it exhibit the same tuberculation as occurs on the antero-dorso-lateral just described. The only reason for disassociating the two specimens specifically is that they represent individuals of somewhat different size; but the disproportion does not appear of itself sufficient ground for separation. The supposed antero-ventro-lateral measures 23 cm. in length by 11 cm. in width at about the middle of the plate. How much of the anterior portion is wanting cannot be accurately determined. Another large specimen from the same locality is to be seen on exhibition in the United States National Museum, at Washington, D. C., bearing the catalogue number 14,821.

Fragments of various size, and indistinguishable from this species so far as one may judge from the ornamentation, have been collected by the writer in the State Quarry fish-bed, near North Liberty, Iowa.[3] Other remains have been found in the Cedar Valley Limestone of the same State by Professor Samuel Calvin. One of the largest of these, which belongs to the State University Museum, shows the posterior portion of the cranium above and below very satisfactorily.

---

[1] Newberry, J. S., Palæozoic Fishes of North America (Monogr. U S. Geol. Surv., Vol. XVI. p. 99), 1889.

[2] The artist has represented these somewhat diagrammatically in Figure 4, with the result of imparting a rougher aspect to the plate than is natural, although it is plain that the original has suffered somewhat from abrasion.

[3] See notes "On the Occurrence of Fossil Fishes in the Devonian of Iowa," appended to Report on the Geology of Johnson County (pp. 108–116), by Samuel Calvin, State Geologist. 1897.

There is good reason for believing that this species also occurs in the Hamilton of New York State. Mr. F. K. Mixer, who has made a careful search for fish remains in the vicinity of Buffalo, has obtained certain fragments from the Encrinal Limestone near the mouth of Eighteen Mile Creek, which exhibit almost precisely the same style of ornamentation, and agree furthermore in size with *D. pustulosus.* One of these fragments is identifiable as the suborbital plate, and shows very distinctly the sensory canals. Another represents about one half of one of the ventro-lateral plates, is rabbeted upon the edges, and shows some variation in the size of its tubercles. Again we notice that tuberculation of the ventral plates bears witness to primitive conditions. The ventro-lateral measures 21 cm. in maximum width, and is traceable for about the same distance in a longitudinal direction, the remaining portion being broken away. It is to be hoped that further and better preserved material will be forthcoming from this horizon, since by reason of their greater antiquity and primitiveness Hamilton Dinichthyids are likely to prove even more interesting than those of Upper Devonian age. In the event of these plates being proved by future discoveries to belong to a species distinct from *D. pustulosus,* with which they are now provisionally associated, it is but fitting to reserve the name *D. mixeri* for the New York species, in honor of the gentlemen to whom we are indebted for our first knowledge of it.

The title of *D. pustulosus,* although misapplied by M. Lohest for *D. tuberculatus,* has never been defined, and we are accordingly at liberty to appropriate it for the present species.

Formation and Locality. — Hamilton Limestone; Wisconsin, Iowa, and New York (?).

In this connection a word may be said concerning another plate discovered by Mr. Mixer, near Sturgeon Point on the shore of Lake Erie. The fossil is embedded in a loose block derived apparently from the Portage Shale, exposures of which occur at this locality. It presents the inferior aspect of a small dorso-median plate, which is worn away anteriorly in such fashion as to reveal an impression of the external surface. This is seen to be finely tuberculated, and a few tubercles are left on an impression of a small plate (antero-dorso-lateral ?) adjoining the first. The longitudinal carina and its terminal process are both indicated, although the latter is partly fractured. The plate is quite thin; and this fact, together with its small size, fine tuberculation, and other characters, renders it probable that it belonged to an immature individual. It may be referred with considerable certainty to *D. ringuebergi,* a species which until the present time has rested upon a solitary dorsal shield from the same locality. Mr. Mixer's specimen is about one fourth smaller than the type, however, and is of more slender construction. If properly regarded as a young individual, it is interesting as being one of the few that are known.

It is evident from the figures of the type specimen of *D. ringuebergi*[1] that the carinal process has been considerably eroded, and the diagram of the inferior surface is not wholly accurate. If the anterior margin is entire, as represented for this species, it covers the region back of the head almost as completely as in *Coccosteus*. The type specimen is preserved in the private collection of its first describer, Mr. E. N. S. Ringueberg, at Lockport, New York. All of the specimens discovered by Mr. Mixer that are mentioned in the present paper are preserved in the collection of the Buffalo Society of Natural Sciences.

Another very beautiful example of a young Dinichthyid is preserved in the Museum of Oberlin College, and through the courtesy of Professor A. A. Wright we have been enabled to reproduce a photograph of it, shown in Plate **5**, Fig. 3. It is only about 5 cm. long, and 4.5 cm. in maximum width; the external surface is non-tuberculated. Unfortunately the terminal process is missing, but the inferior carina is very distinct. It is also seen to be strongly emarginate in front.

The drawings for Plates **1** to **3** have been executed by Messrs. C. A. King and J. W. Folsom. Plates **4** and **5** are reproduced from photographs of the original specimens, taken by Dr. T. A. Jaggar, Jr., excepting Figure 3 of Plate **5**.

---

[1] Amer. Journ. Science, [3], Vol. XXVII. p. 477, June, 1884.

LIST OF AMERICAN SPECIES OF DINICHTHYS.

1. *D. canadensis* Whiteaves,	Upper Devonian, Manitoba.
2. *D. clarki* Claypole,	Cleveland Shale, Ohio.
3. *D. corrugatus* Newberry,	Cleveland Shale, Ohio.
4. *D. curtus* Newberry,	Cleveland Shale, Ohio.
5. *D. gouldi* Newberry,	Cleveland Shale, Ohio.
6. *D. gracilis* Claypole,	Cleveland Shale, Ohio.
7. *D. hertzeri* Newberry,	Huron Shale, Ohio.
8. *D. ingens* Wright (MS.),	Cleveland Shale, Ohio.
9. *D. intermedius* Newberry,	Cleveland Shale, Ohio.
10. *D. kepleri* Claypole,	Cleveland Shale, Ohio.
11. *D. lincolni* Claypole,	Marcellus Shale, New York.
12. *D. minor* Newberry,	Cleveland Shale, Ohio.
13. *D. newberryi* Clarke,	Genesee and (?) Portage Shales, New York.
14. *D. precursor* Newberry,	Corniferous Limestone, Ohio.
15. *D. prentis-clarki* Claypole,	Cleveland Shale, Ohio.
16. *D. ringuebergi* Newberry,	Portage Shale, New York.
17. *D. terrelli* Newberry,	Cleveland Shale, Ohio.
18. *D. tuberculatus* Newberry,	Chemung Group, Pennsylvania.
19. *D. pustulosus* nobis,	Hamilton Limestone, Wisconsin, Iowa, and (?) New York.

BIBLIOGRAPHY.

Pander, C. H.
1857. Ueber die Placodermen des devonischen Systems. St. Petersburg.

Barrande, J.
1872. Système Silurien du centre de la Bohême. Vol. I. Supplement.

Newberry, J. S.
1873. Report Geological Survey of Ohio, Palæontology. Vol. I.

Newberry, J. S.
1875. Report Geological Survey of Ohio, Palæontology. Vol. II.

Kayser, E.
1880. Dinichthys eifeliensis. Zeitschr. deutsch. geol. Gesellsch., Vol. XXXII. p. 818.

Koenen, A. von.
1883. Beitrag zur Kenntniss der Placodermen. Abhandl. kön. Gesell. Wissensch. Göttingen, Vol. XXX.

Clarke, J. M.
1885. On the higher Devonian Faunas of Ontario County, New York. Bull. U. S. Geol. Surv., No. 16, pp. 35–120.

Lohest, M.
1888. Recherches sur les Poissons des Terrains Paléozoiques de Belgique. Ann. Soc. Géol. Belg., Vol. XV. pp. 112–203. [See especially "Résultats Géologiques," etc., pp. 168–196.]

Traquair, R. H.
1889. Homosteus, Asmuss, compared with Coccosteus, Agassiz. Geol. Mag., [3], Vol. VI. pp. 1–8, Plate I.

Newberry, J. S.
1889. The Palæozoic Fishes of North America. Monogr. U. S. Geol. Surv., Vol. XVI.

Trautschold, H.
1889. Ueber Coccosteus megalopteryx Trd., Coccosteus obtusus und Cheliophorus verneuili Ag. Zeitschr. deutsch. geol. Gesellsch., Vol. XLI. pp. 35–48, Plates III.–VI.

Trautschold, H.
1890. Ueber Megalopteryx und Pelecyphorus. Zeitschr. deutsch. geol. Gesellsch., Vol. XLII. p. 575.

Jaekel, O.
1890. Ueber Coccosteus. Zeitschr. deutsch. geol. Gesellsch., Vol. XLII. p. 776.

Traquair, R. H.
1890. On the Structure of Coccosteus decipiens Ag. Ann. Mag. Nat. Hist., [6], Vol. V. pp. 125–136, Plate X. [Literature references, pp. 135, 136.]

Woodward, A. S.
1891. Catalogue of Fossil Fishes in the British Museum. Part II.

Gürich, G.
1892. Ueber Placodermen und andere devonische Fischreste im Breslauer mineralogischen Museum. Zeitschr deutsch. geol. Gesellsch., Vol. XLII. pp. 902–912.

Wright, A. A.
1893. On the Ventral Armor of Dinichthys. Report Geol. Surv. Ohio, Vol. VII. pp. 620–626, Plate XLIV.

Wright, A. A.
1894. The Ventral Armor of Dinichthys. Amer. Geol., Vol. XIV. pp. 313–320, Plate IX.

Koenen, A von.
1895. Ueber einige Fischreste des norddeutschen und böhmischen Devons. Abhandl. k. Gesell. Wissensch. Göttingen, Vol. XL. pp. 1–37, Plates I.–V.

Dean, B.
1895. Fishes, Living and Fossil. New York, pp. 129–138.

Dean, B.
1896. On the Vertebral Column, Fins, and Ventral Armoring of Dinichthys. Trans. N. Y. Acad. Sci., Vol. XV. pp. 157–163, Plates VII., VIII.

Eastman, C. R.
1896. Preliminary Note on the Relations of certain Body-Plates in the Dinichthyids. Amer. Journ. Science, [4], Vol. II. pp. 46–50.

Eastman, C. R.
1896. Observations on the Dorsal Shields in the Dinichthyids. Abstract in Amer. Geol., Vol. XVIII. pp. 222, 223.

Dean, B.
1897. Additional Note on the Ventral Armoring of Dinichthys. Trans. N. Y. Acad. Sci., Vol. XVI. pp. 57–60, Plate III.)

Wright, A. A.
1897. New Evidence upon the Structure of Dinichthys. Fifth Ann. Rep. Ohio State Acad. Sciences, pp. 59, 60.

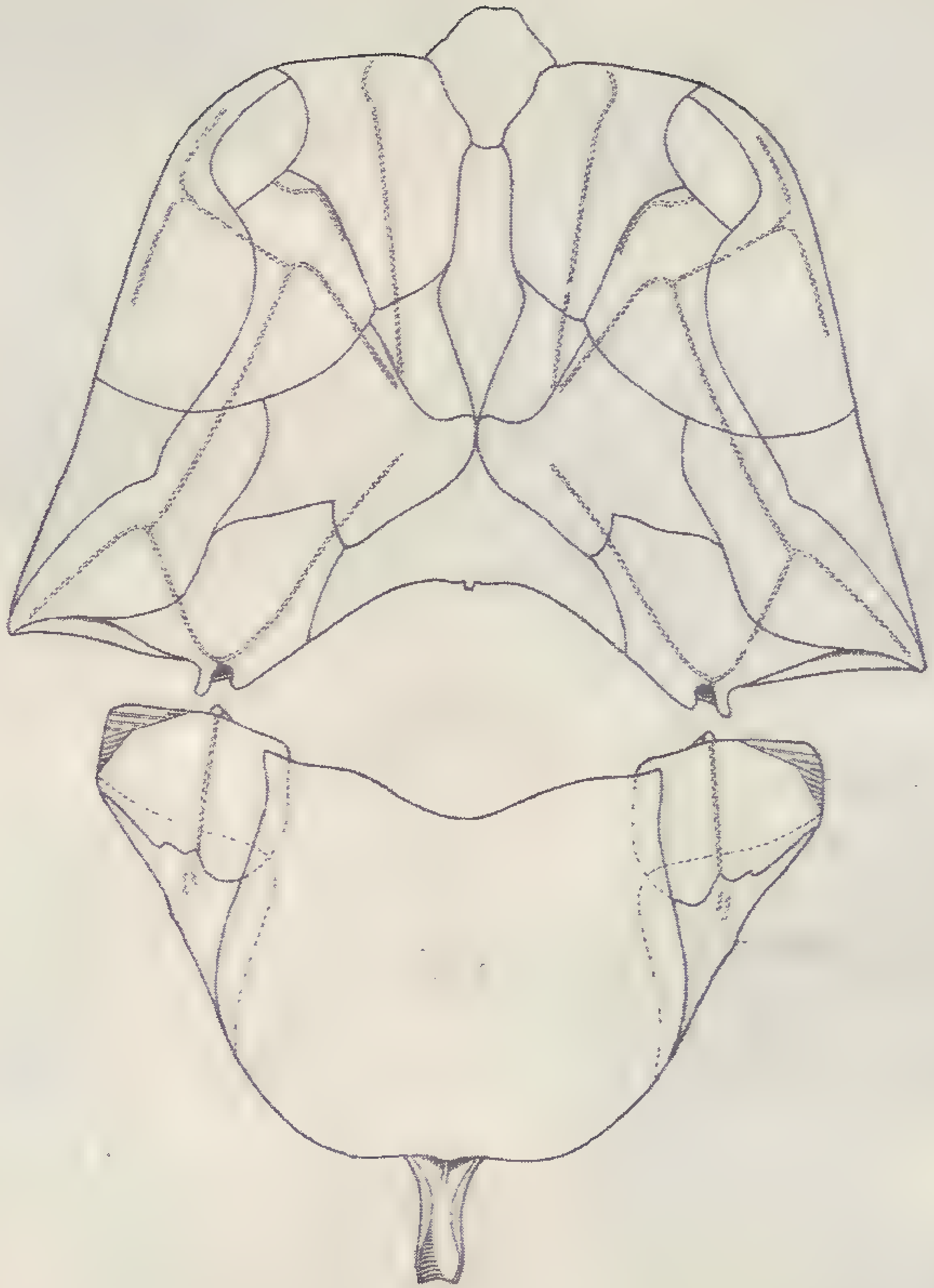
PLATE 1.

Fig. 1. *Dinichthys intermedius* Newb. × ⅓. Projection of cranium and dorsal plates in their natural relations with respect to one another. *DM,* Dorso-median; *ADL,* Antero-dorso-lateral; *PDL,* Postero-dorso-lateral. Sensory canals indicated by double dotted lines, boundaries of plates by single lines. The posterior process depends at an angle of about 60° from the plane of the dorso-median.

Fig. 2. *Dinichthys* (?) *newberryi* Clarke. × ⅓. Restoration of the Portage plastron shown in Plate 4. *AVM,* Antero-ventro-median; *PVM,* Postero-ventro-median; *AVL,* Antero-ventro-lateral; *PVL,* postero-ventro-lateral. Radiating lines show approximately the course of vascular canals. Overlapped borders of plates indicated by dotted lines.

PLATE I.

1.



2.

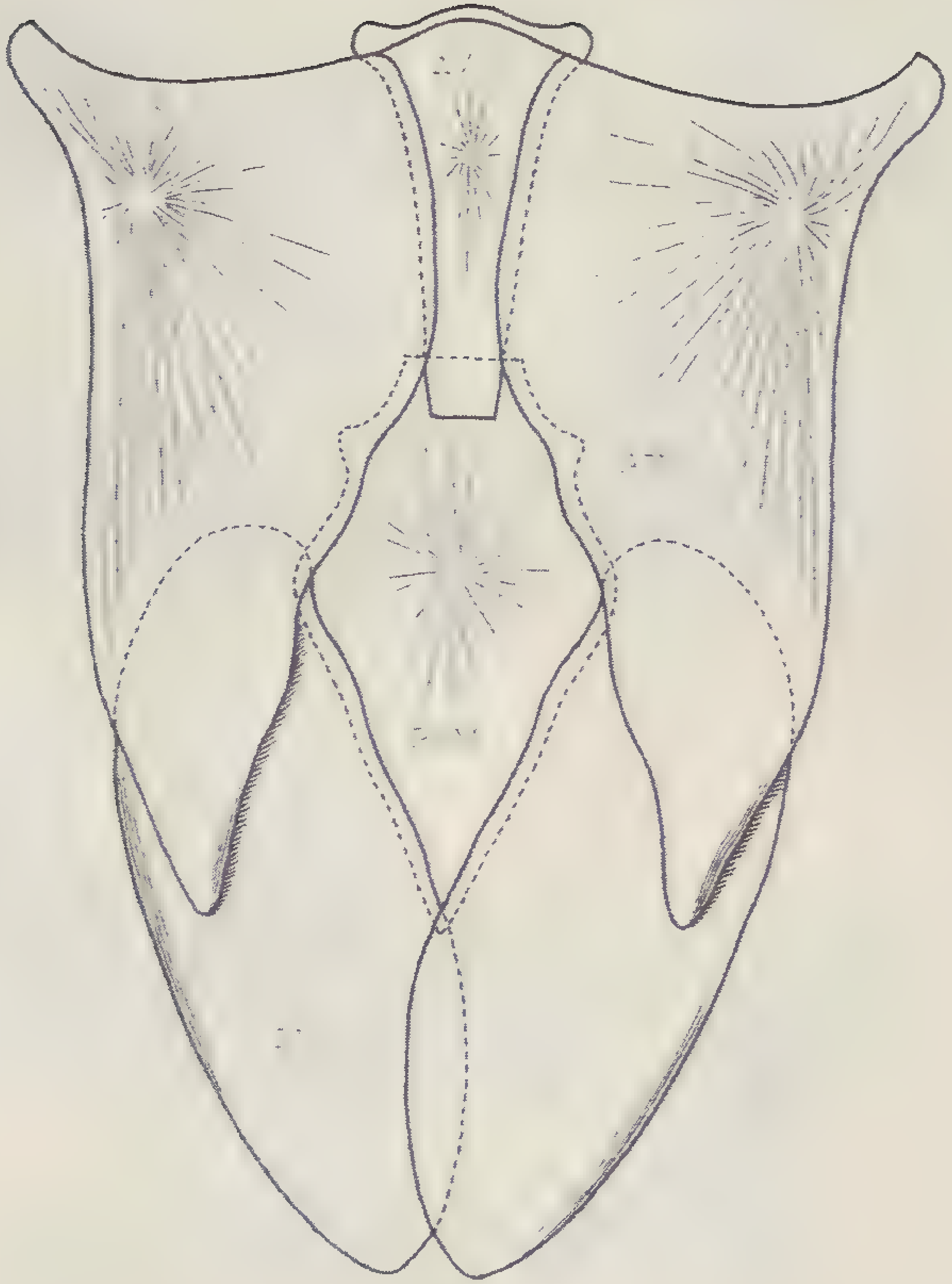


PLATE 2.

Fig. 1. *Dinichthys terrelli* Newb. $\times \frac{1}{4}$. Cleveland Shale; Lindale, Ohio. M. C. Z., Cat. No. 1379. Fragment showing internal surface of antero- and postero-dorso-lateral plates preserved in natural association with each other. Their union by pegs and sockets, the sinuous lateral boundary of the posterior plate, and the base of articulating condyle of the antero-dorso-lateral, are noteworthy features.

Fig. 2. Postero-ventro-median plate of an indetermined Dinichthyid species, from the Cleveland Shale of Lorain County, Ohio. $\times \frac{1}{5}$ (approximately). M. C. Z., Cat. No. 1300. The external surface, shown here, bears impressions of overlapping plates, and is notched in front for reception of the antero-ventro-median.

Fig. 3. *Dinichthys bohemicus* (Barr.). $\times \frac{2}{3}$. Middle Devonian (Étage Gg^1); Svagerka, Bohemia. M. C. Z., Cat. No. 1377. Tuberculated dorso-median plate. The posterior portion of the specimen, which was fractured obliquely downward, has been ground smooth and polished, so as to show the inferior carina in section.

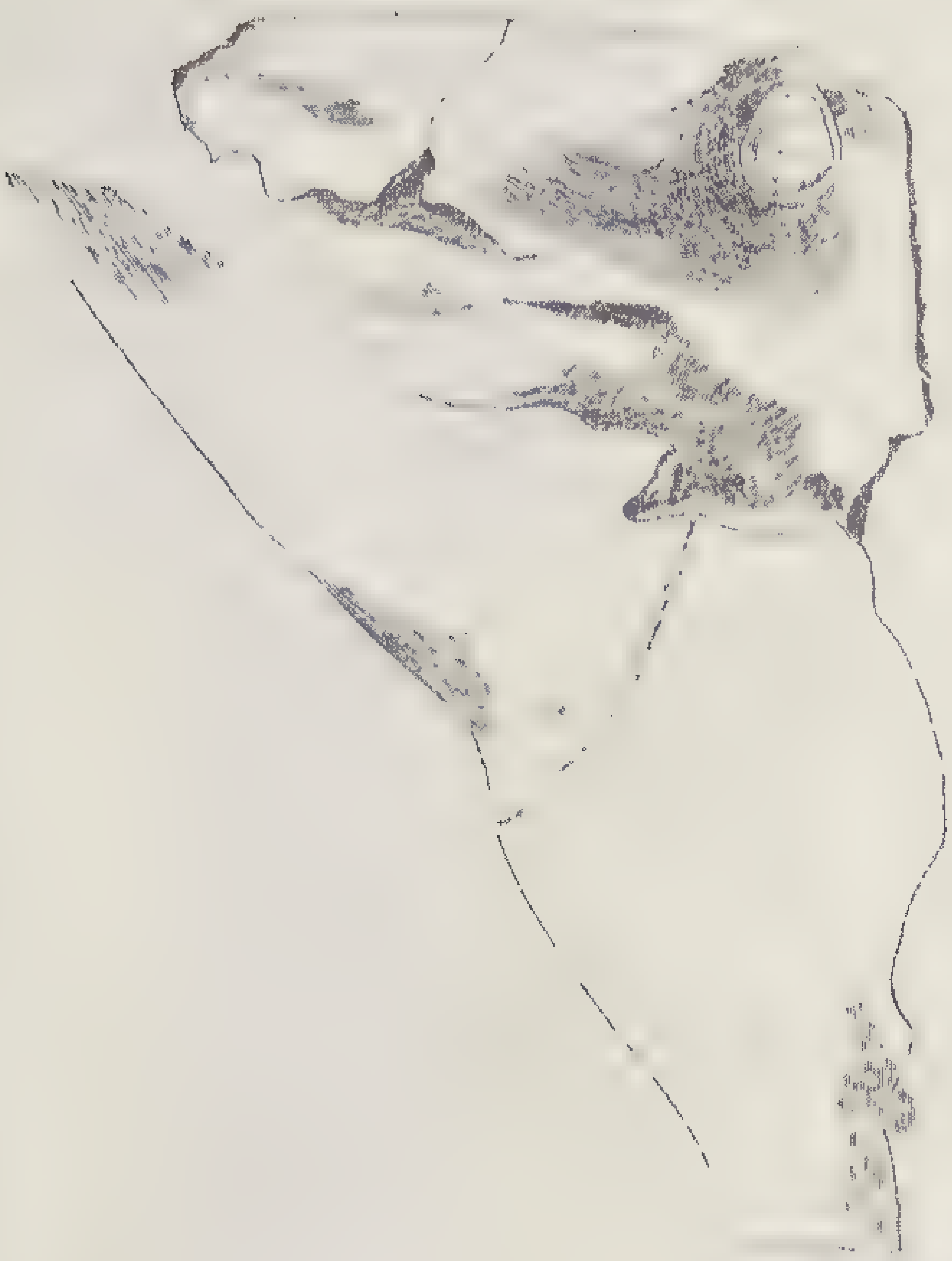
Fig. 4. *Dinichthys pelmensis* sp. nov. $\times \frac{1}{1}$. Middle Devonian; Pelm, Eifel District. M. C. Z., Cat. No. 1375. Dorso-median plate with perfectly preserved carinal process, and faint indications of sensory canals.

Fig. 5. *Dinichthys terrelli* Newb. $\times \frac{1}{5}$. Cleveland Shale; Lorain County, Ohio. M. C. Z., Cat. No. 1301. Antero-ventro-median plate, seen from the external surface. Thickness at posterior tip less than 2 mm.; the plate has every indication of being entire, or very nearly so.

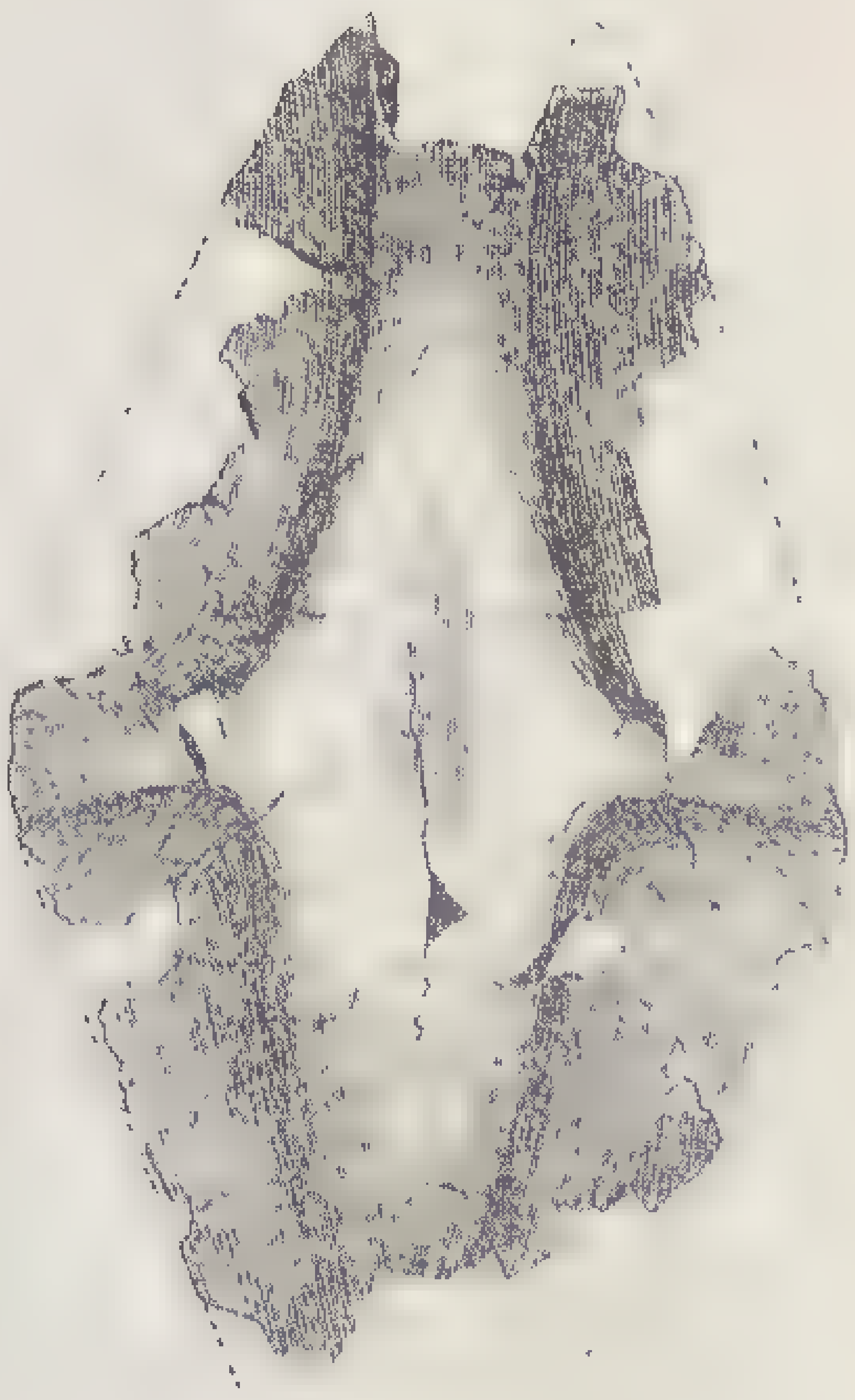
Fig. 6. Same specimen as shown in Fig. 5, viewed from the internal or visceral side. The thickened T-shaped ridge seen on this surface is very characteristic.

2.

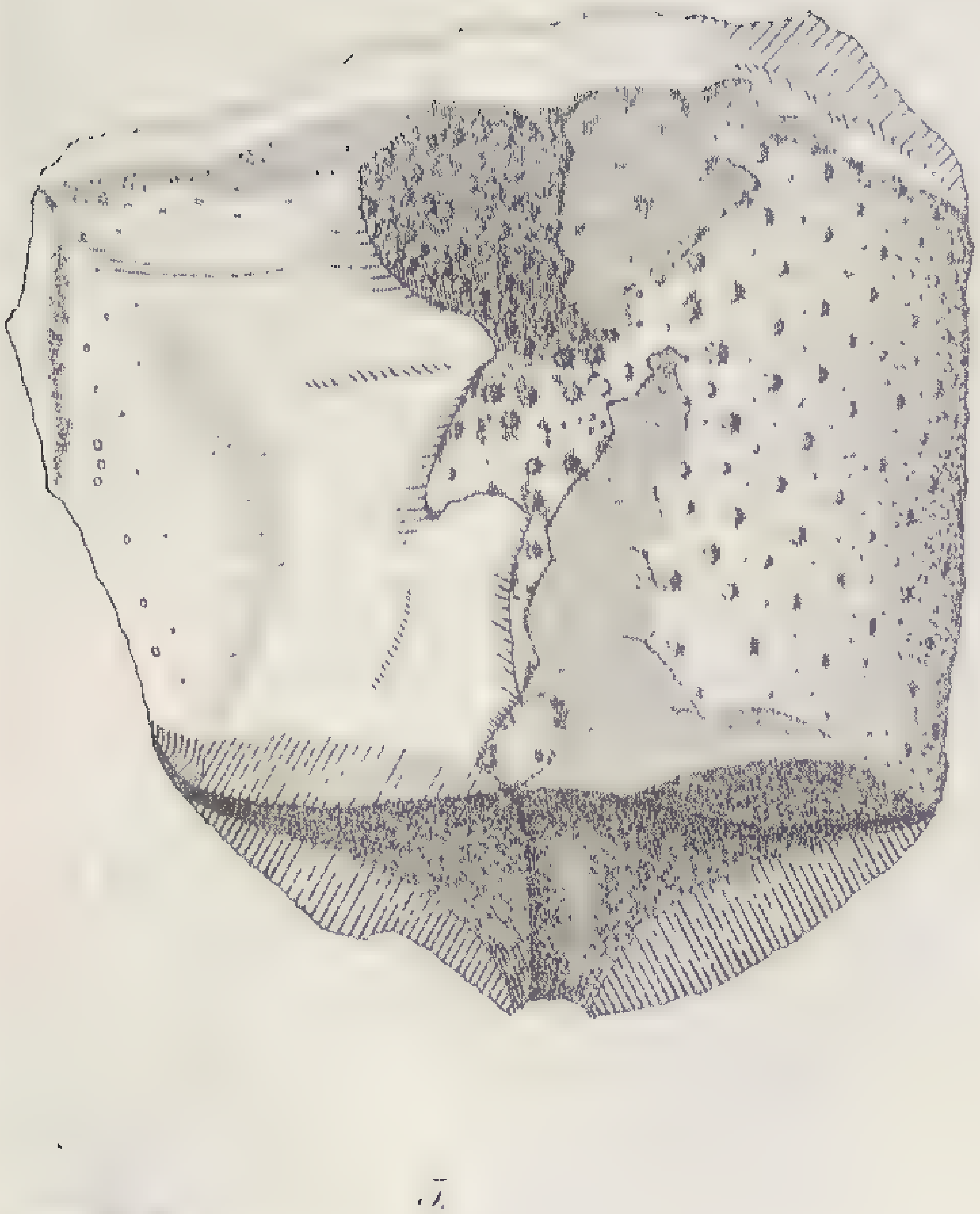
1



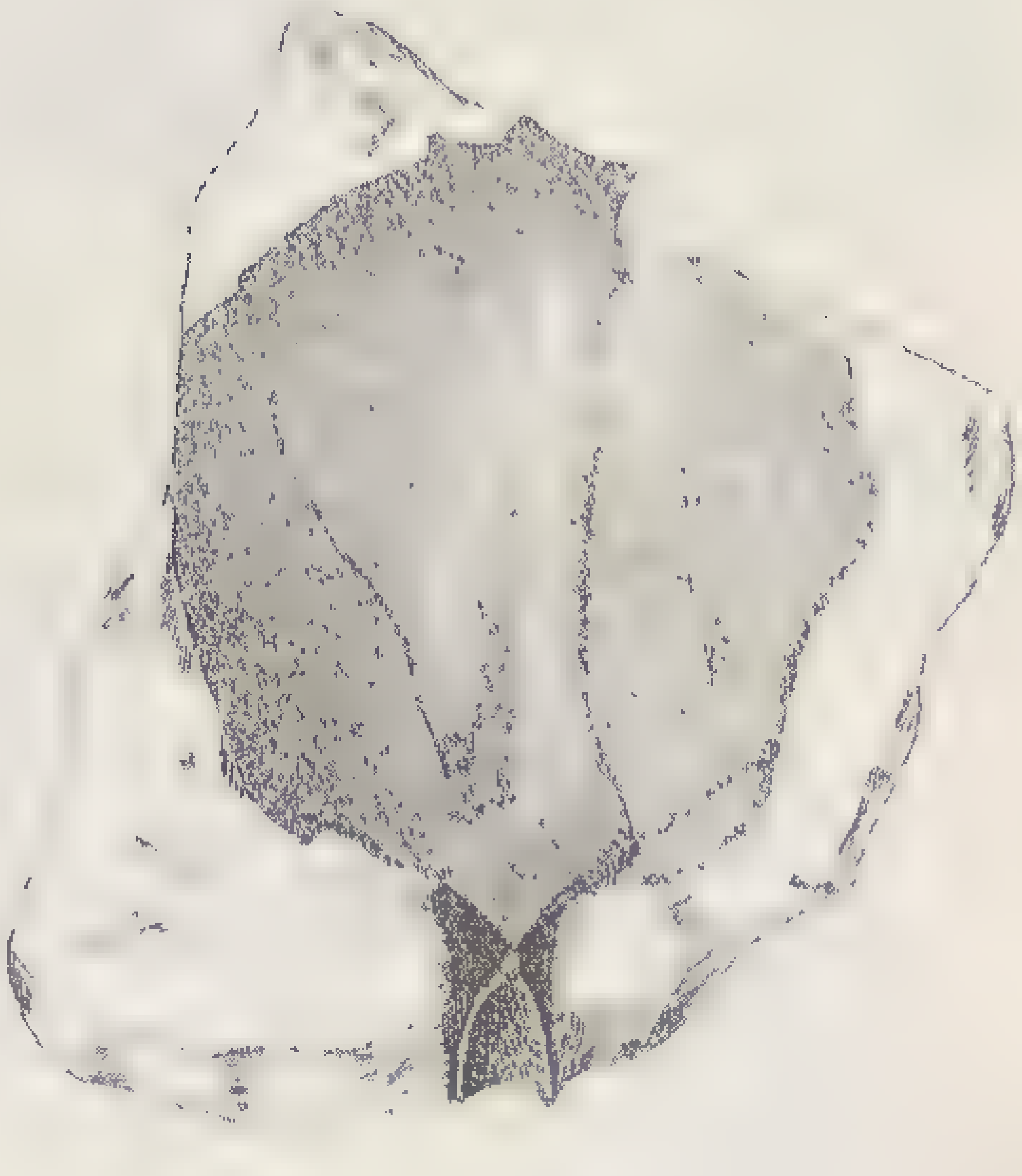
2



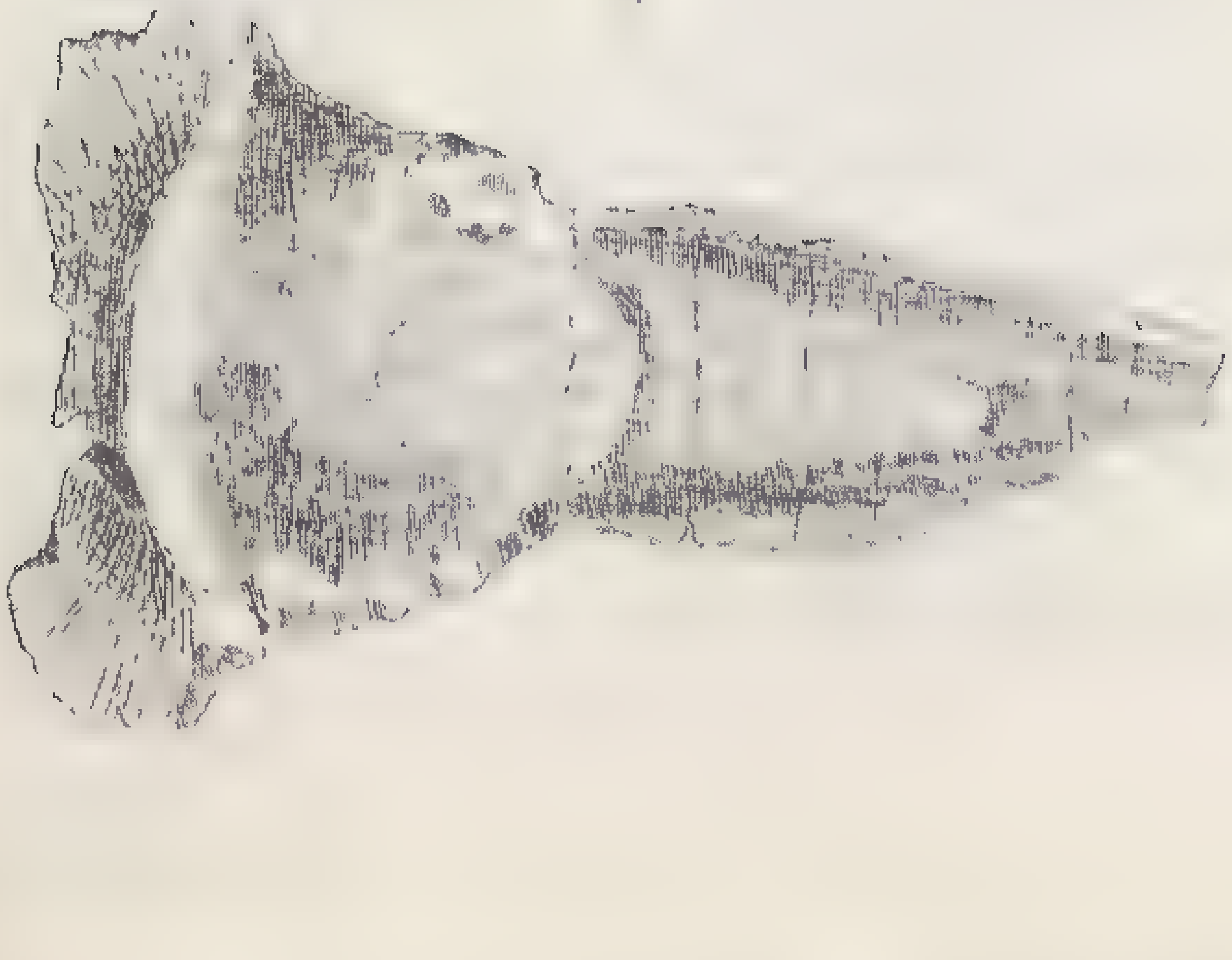
3



4



5



6

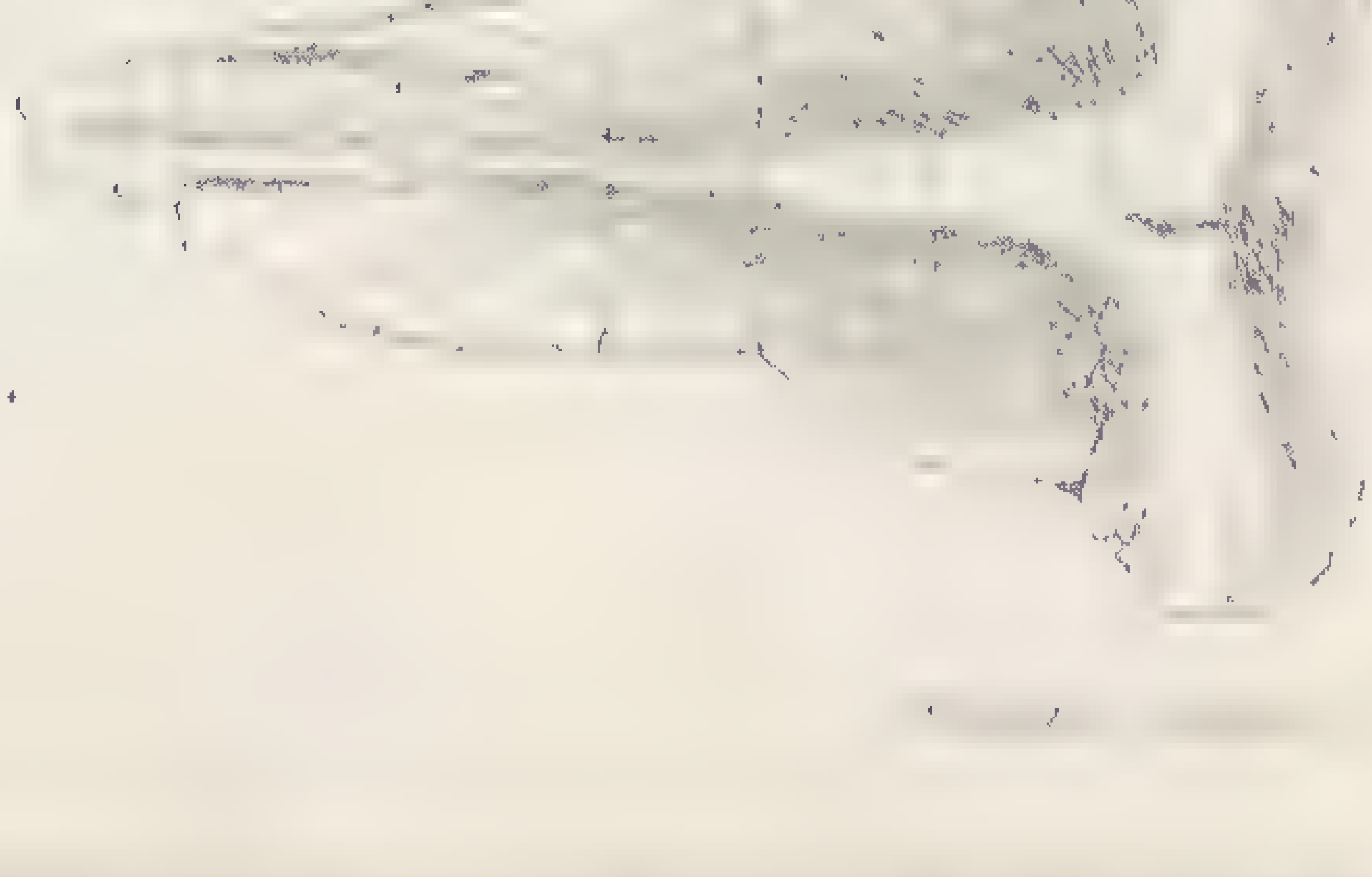


PLATE 3.

Fig. 1. *Dinichthys* (?) *intermedius* Newb. × $\frac{3}{4}$. Cleveland Shale; Lindale, Ohio. M. C. Z., Cat. No. 1380. External aspect of supposed antero-ventro-median plate.

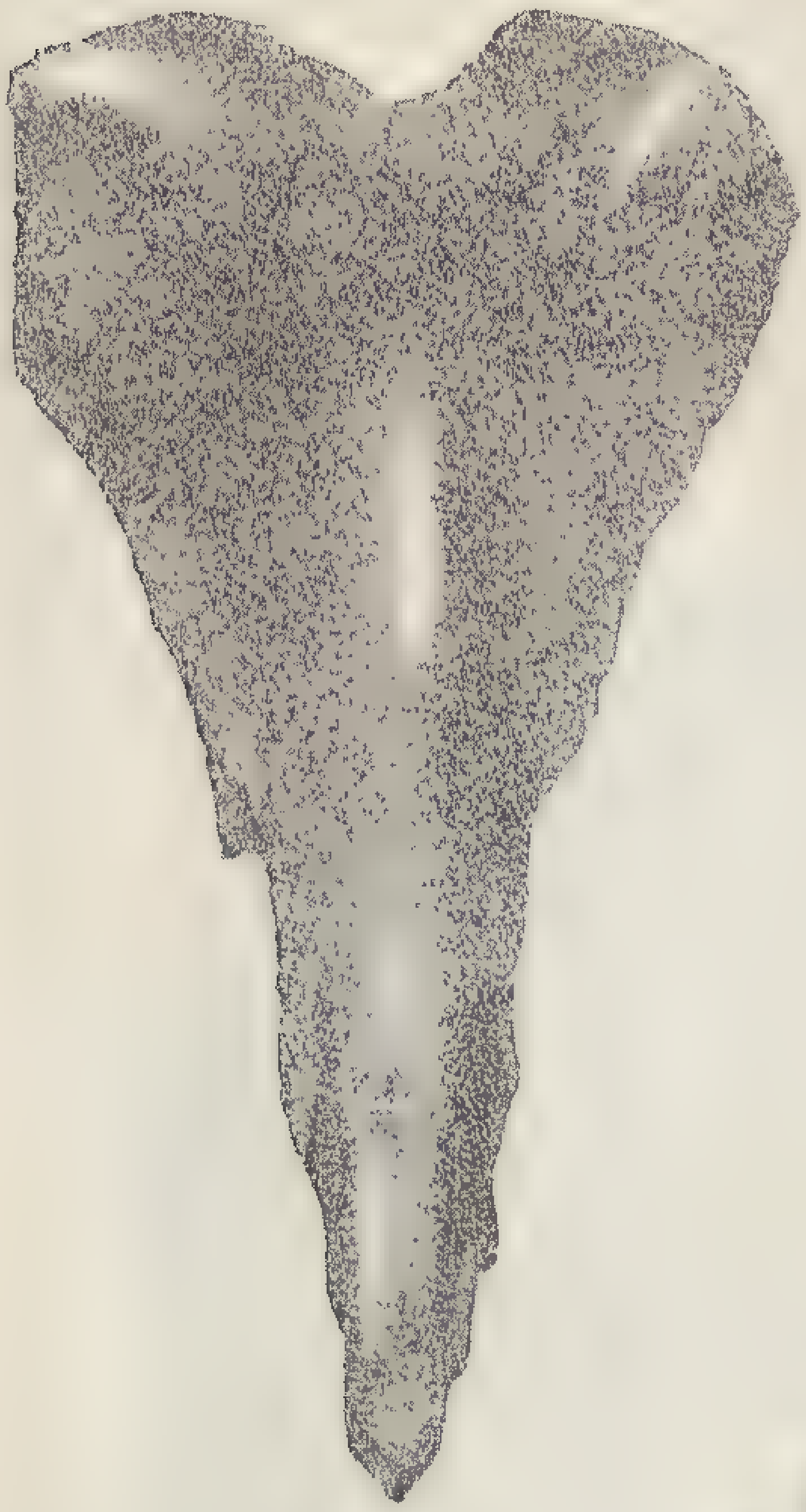
Fig. 2. *Dinichthys terrelli* Newb. × $\frac{1}{3}$. Cleveland Shale; Lorain County, Ohio. M. C. Z., Cat. No. 1315. Posterior aspect of carinal process belonging to a large-sized dorso-median, viewed in a vertical position. The semicircular incision below, where it overrode the vertebral axis, its massive character, and depth of posterior cavity, are remarkable. It projects downward and backward at an angle of about 60° with the plane of the dorso-median, traced along the median line of the back.

Fig. 3. *Dinichthys eifeliensis* Kayser. × $\frac{1}{1}$. Middle Devonian; Berndorf, near Hillesheim, Eifel District. M. C. Z., Cat. No. 1374. Carinal process detached from dorso-median plate.

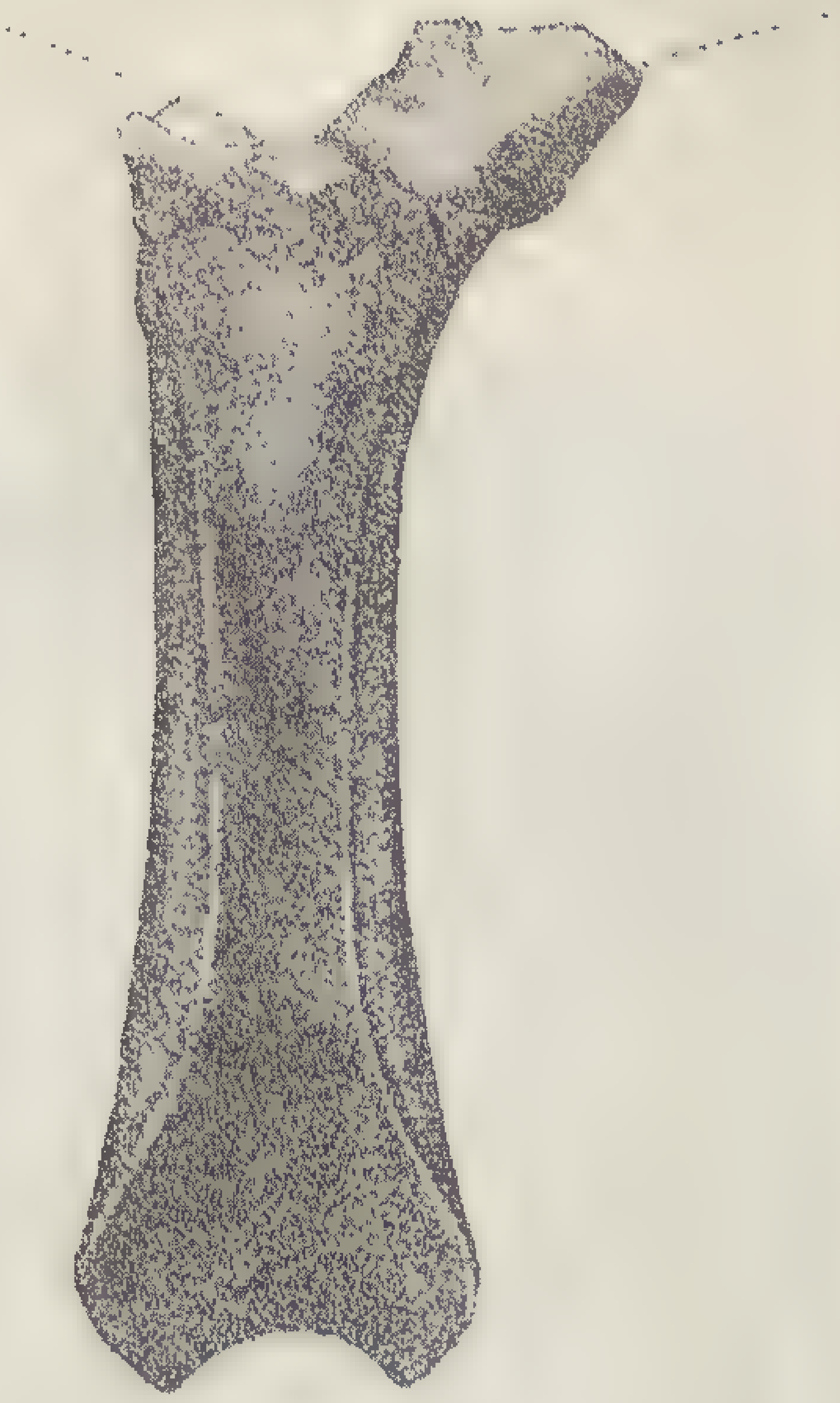
Fig. 4. *Dinichthys pustulosus* sp. nov. × $\frac{1}{1}$. Hamilton Limestone; Cement Quarries, Milwaukee, Wisconsin. M. C. Z., Cat. No. 1381. Slightly abraded antero-dorso-lateral plate, showing single sensory canal, and relatively fine tuberculation.

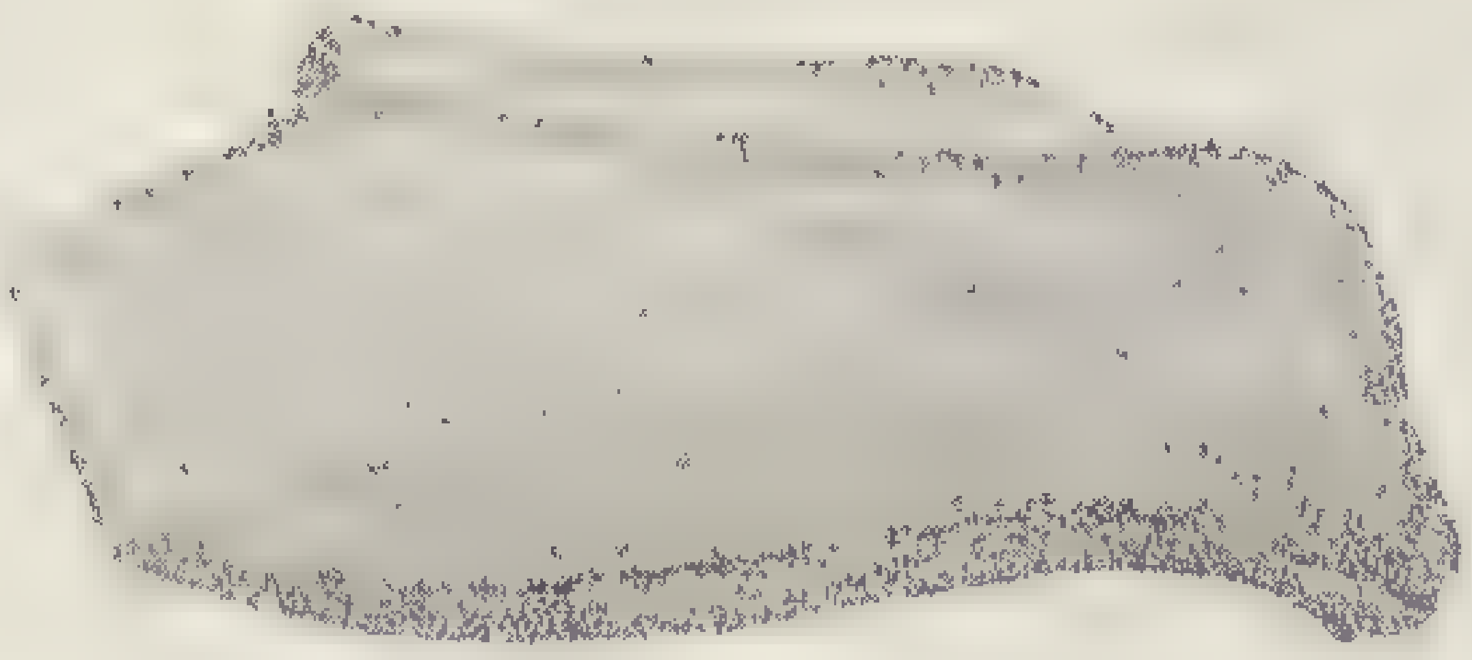
PLATE 3.

1.

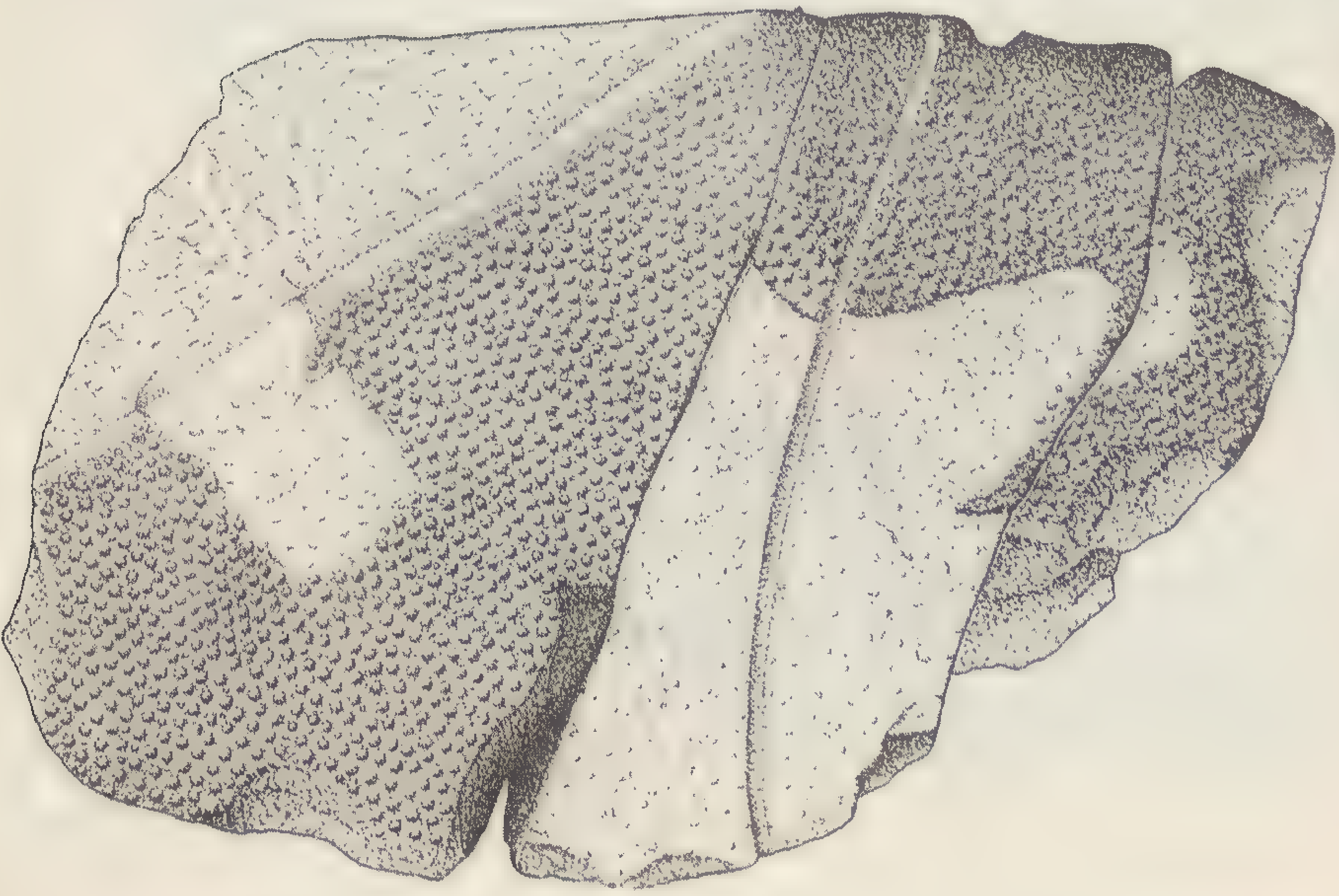


2.





4.



[illegible]

PLATE 4.

Dinichthys (?) *newberryi* Clarke. × $\frac{1}{3}$. Portage Shale; Sturgeon Point, near Buffalo, New York. Weathered plastron and associated fragments. Reproduced from a photograph without retouching.

PLATE 5.

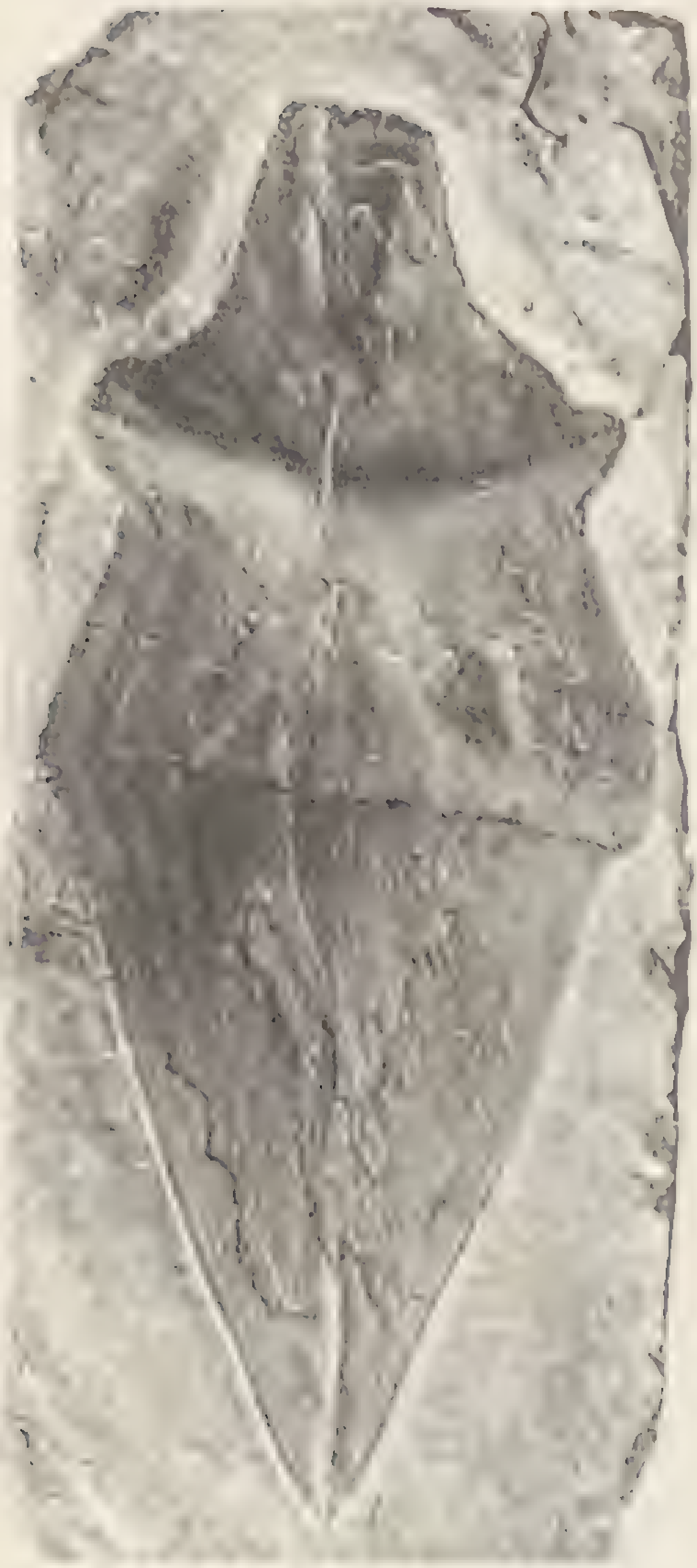
Fig. 1. Postero-ventro-median plate of an unknown Dinichthyid species. × $\frac{2}{5}$ (approximately). M. C. Z., Cat. No. 1475. This plate is preserved in counterpart, and a portion of the bone adheres to the opposite side.

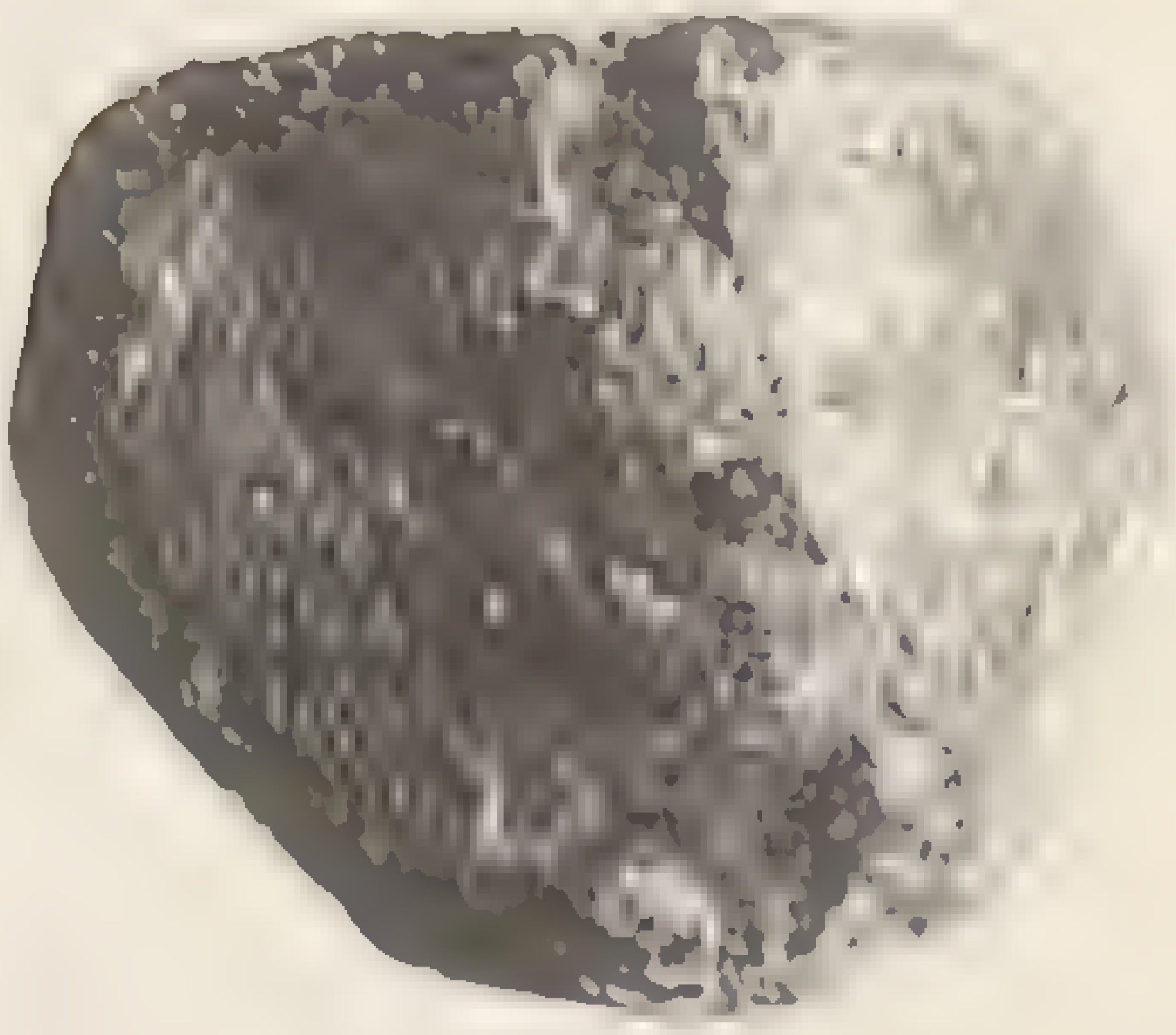
Fig. 2. *Dinichthys* (?) *bohemicus* (Barr.). × $\frac{1}{3}$. Middle Devonian (Étage Gg^1); Chotec, Bohemia. M. C. Z., Cat. No. 1376. Detached dorso-median plate, more highly arched and rounded in outline than that shown in Plate **2**, Fig. 3, but having the same ornamentation. The carinal process is slender, and appears only in section where the matrix has been ground away.

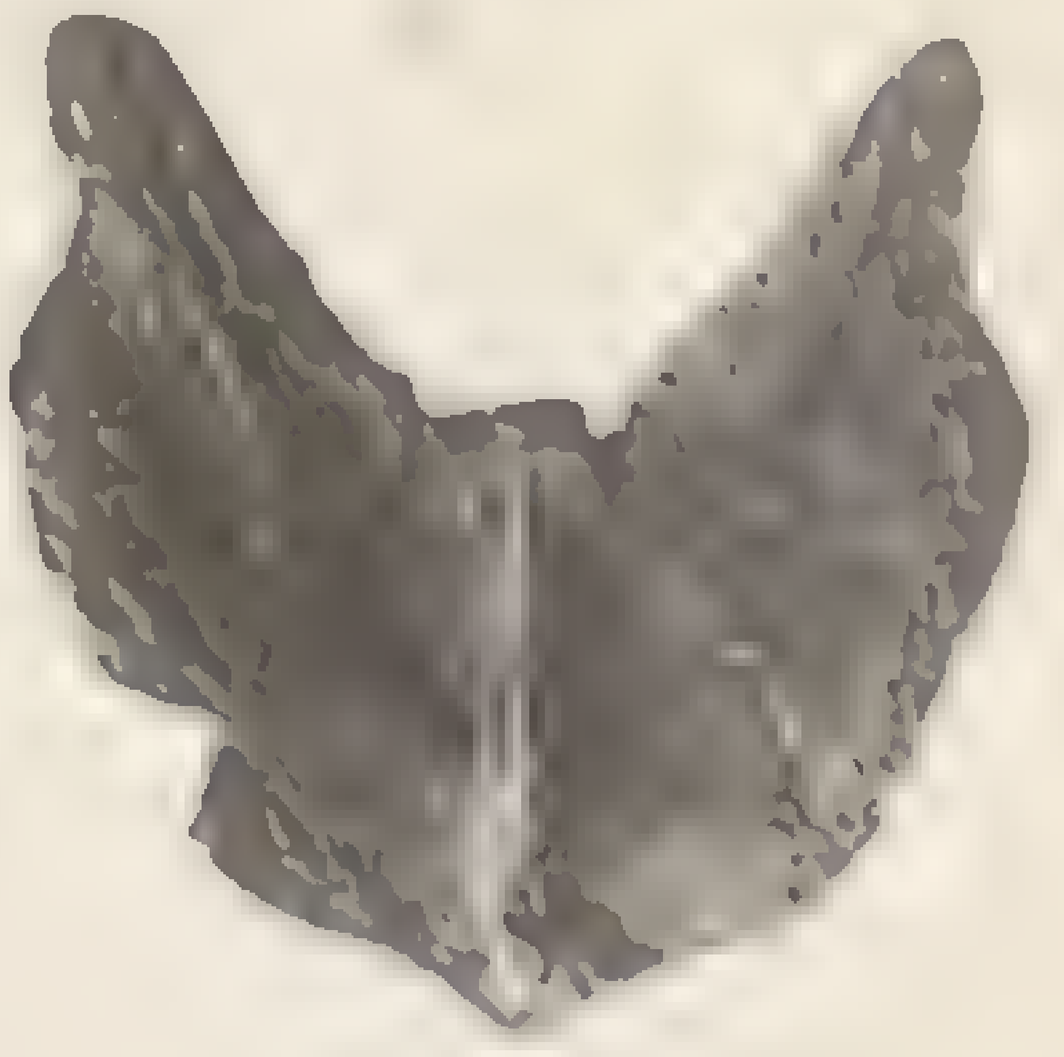
Fig. 3. Dorso-median plate of a young individual representing an unknown Dinichthyid species, seen from the under side. × $\frac{3}{4}$. Cleveland Shale; vicinity of Cleveland, Ohio. Original preserved in Museum of Oberlin College.

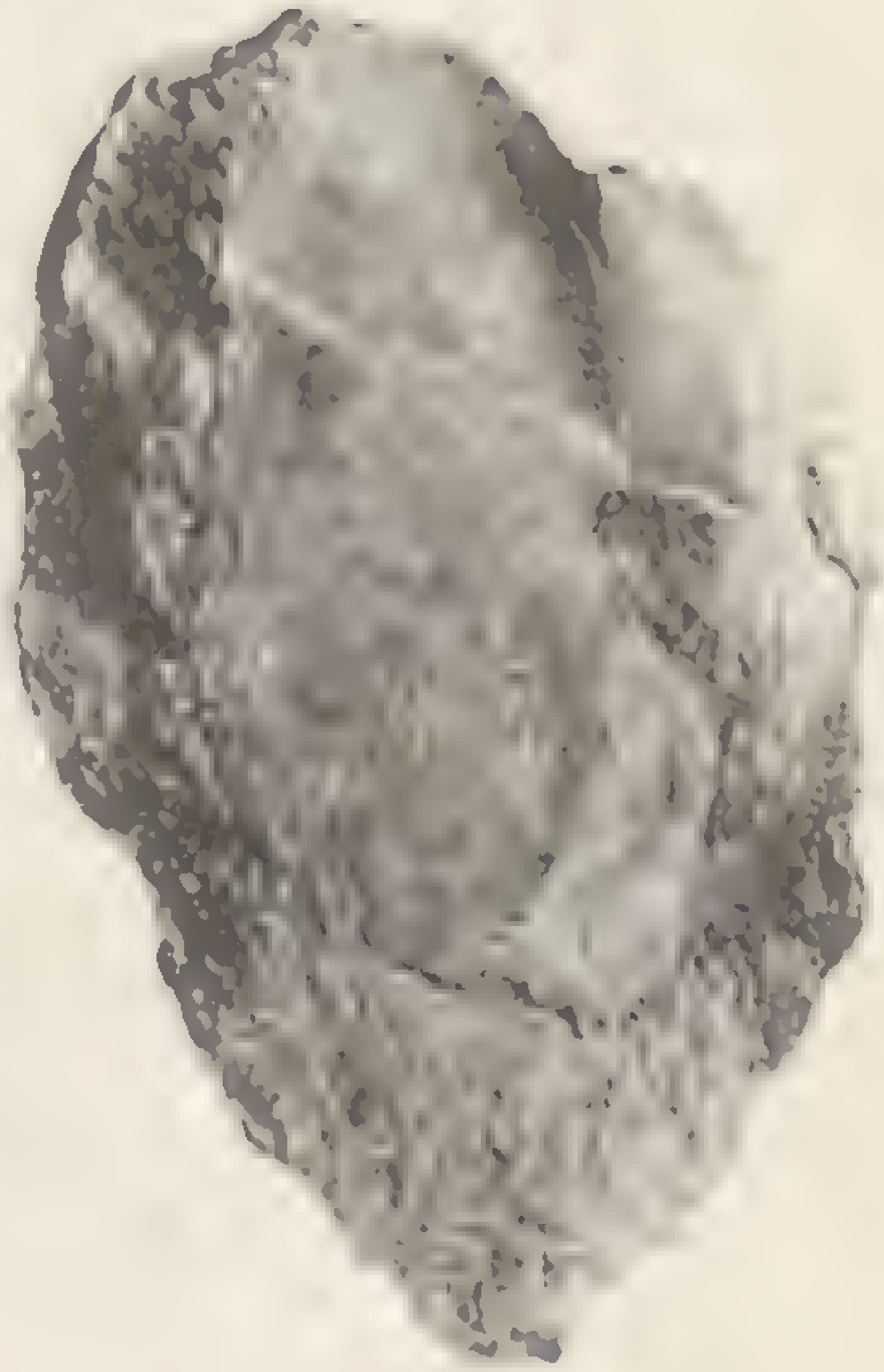
Fig. 4. *Dinichthys eifeliensis* Kayser. × $\frac{1}{3}$. Middle Devonian; Eifel District. Internal aspect of right antero-ventro-lateral plate. M. C. Z., Cat. No. 1474.

1









Bulletin of the Museum of Comparative Zoölogy
AT HARVARD COLLEGE.
VOL. XXXI. NO. 3.

TRICHONYMPHA, AND OTHER PARASITES OF TERMES FLAVIPES.

BY JAMES F. PORTER.

WITH SIX PLATES.

CAMBRIDGE, MASS., U. S. A.:
PRINTED FOR THE MUSEUM.
OCTOBER, 1897.

No. 3. — *Trichonympha, and other Parasites of Termes flavipes.*

By James F. Porter.[1]

Contents.

1. Trichonympha agilis 48
2. Pyrsonympha vertens 59
3. Dinenympha gracilis 65
4. Gregarinida 65
Papers Cited 67
Explanation of Plates 68

Nearly twenty years ago Dr. Joseph Leidy ('77) discovered several new and quite distinct species of Protozoa living parasitic in the intestine of Termes flavipes.[2] A few years later he ('81) published an extended account of these strange creatures, accompanied by a large number of drawings illustrating the great variety of forms which they assume. Some of these parasites, to which he gave the name Trichonympha agilis, were so unlike any previously described Protozoa that their discoverer was not entirely certain where they ought to be classed; at first ('77) he regarded them as "probably related with the Turbellaria on the one hand, and by evolution with the Ciliate Infusoria on the other." Later ('81, p. 529), however, he was disposed to view this parasite as having a character intermediate between a ciliate infusorian and a gregarine, but (p. 436) more nearly related to the gregarines.

Since then W. Saville Kent ('85) has made some additional observations on the structure and habits of this parasite from material sent to him by Dr. Leidy, and has also discovered a very similar parasite, to which he gave the name Trichonympha leidyi, in the White Ant of Tasmania.

Besides these studies on Trichonympha, there have appeared descriptions of some other forms which seem to be closely related to this genus. I refer to Joenia, described by Grassi ('85), and to Lydionella, found by Frenzel ('91), both parasitic in the intestine of Termites. The paper by

---

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, under the direction of E. L. Mark, No. LXXXIV.

[2] Some of these had been previously seen by Lespès ('56); but he alluded to them only briefly (pp. 237, 258) in his memoir. Compare Leidy ('81, pp. 425–428).

Frenzel is especially important, because it gives a careful account of the structural conditions of the genus studied by him, though even he did not make use of sections to ascertain the minuter details of structure.

At the suggestion of Dr. Mark, I began in the autumn of 1895 an investigation of this peculiar and interesting parasite of Termes flavipes, in the hope of being able, by means of more recent methods, — especially sectioning, — to add something to what was already known concerning them. An excellent 1.5 mm. homogeneous immersion by Zeiss has been of much value to me in studying the minute details of structure. In October I captured some of the White Ants, both "workers" and "soldiers," in the woods near Cambridge, and on opening the intestine of one of them found it swarming with the same kinds of parasites that Leidy had discovered in his New Jersey Termites.

1. Trichonympha agilis.

Plate 1: Plate 2; Plate 3, Figs. 24-26.

I have represented in Figures 1 and 2 what seem to me fairly normal and characteristic appearances of a quiescent T. agilis, and in Figure 3 a view of the head end, seen from the anterior pole. My figures should be considered, however, simply as in a measure supplementary to those of Leidy. His observations were so careful and accurate that I have almost no modifications or corrections of his description to suggest; but I shall be able to add something to his account.

Upon seeing one of these peculiar animals, the question immediately arises, Wherefore such a remarkable cloak of cilia? Well developed locomotor organs are the last thing one would expect to find in a parasite whose food is close at hand and whose field of exploration is so limited. With the hope of getting some light on this question, and wishing at the same time to discover, if possible, the situation of the mouth, I experimented by putting living specimens into various fluids; among others, into very much diluted milk. The Trichonymphæ immediately on escaping from the intestine began ploughing their way through the milk corpuscles, passing across the field of the microscope so rapidly that, in order to follow them, it was necessary to keep the slide in constant motion. The various courses traversed by them were indicated by paths cleared of the oil globules. Upon watching their movements, it presently became apparent that the shortest and most anterior cilia were to a very large extent responsible for the motion. The longer cilia, those extending backwards to about the region of the posterior end of the body (Figs. 1, 2) vibrated but little, while the very long cilia that enveloped the posterior half of the animal and reached out far behind (Figs. 1, 2) appeared to be absolutely motionless. These last are not quite useless, however, for I noticed that milk corpuscles began to be entangled among them, and soon afterward long trains of globules were being dragged behind each animal (Figs. 6 and 4). At first I thought this was merely accidental, but after longer observation I came to the conclusion that the cilia actually enfold the globules, for these are gradually drawn in towards the animal, and finally come to lie in close contact with the posterior part of its body (Figs. 4, 5). That the cilia are prehensile in their nature has already been observed by Kent, for he says: "When placed in diluted milk, the animalcules of both the American and Tasmanian species of Trichonympha have been observed by me to assume a fixed condition that has not hitherto been described. An attachment to the surface of organic substances or other convenient fulcra is then accomplished through the medium of the long fascicle of hair-like cilia that are produced from their posterior extremity. These cilia, intersecting one another at a short distance from the body, form a sort of hollow cone, the expanded base of which grasps the selected fulcrum of support after the manner of an acetabulum. This habit of, as it were, anchoring themselves by their long caudal cilia was observed in both the adult and the immature animalcules."

I have observed that Trichonympha may attach itself even to the cover glass by means of its cilia. This evident habit of grasping things by means of the caudal cilia suggested the idea that these cilia might perhaps have the function not only of attaching the animal to the host, but also of procuring food; however, I must acknowledge that it appeared highly improbable that these seemingly motionless cilia, which clothe and tightly invest the animal, could have a function which ordinarily requires so much activity; furthermore, I had been unable thus far to find any mouth opening. Kent in his article says (p. 271): "An important point that was left undetermined by Dr. Leidy respecting the structure of Trichonympha relates to the precise position of the oral aperture. The bodies of the animalcules are almost invariably filled with fragments of the woody débris devoured by their hosts, the White Ants, which shows that their sustenance is taken into their body in a solid state, and is not simply absorbed in the fluid form, as occurs with the group of the Opalinidæ. A prolonged observation of living examples of the American species remitted me by Dr. Leidy, and likewise of the Tasmanian type here introduced, has resulted in my determining that a distinct oral aperture is developed upon one side of the body at a short distance only from the apical extremity. This orifice takes the form of a transverse slit, and is followed by a narrow œsophageal tract which opens into the capacious digestive cavity that occupies one half or two thirds of the posterior region of the body. The plan recommended by Dr. Leidy for observing the vital phenomena of these animalcules is to empty out the intestine of the White Ant containing them into a little white of egg. I also have found this material favorable for their observation, but have gained an additional insight into their life history by employing in a like manner thinly diluted milk. In this medium they not only live for a considerable time, but meet with abundant nutriment, their pharynx and digestive cavity being frequently found densely packed with its component corpuscles after their immersion in this fluid for a short interval."

Unfortunately, Kent does not give any figures, and I have been unable to discover in the living animals the mouth he describes. However, the existence of such a structure could, I imagined, be easily determined by means of sections. These I endeavored to procure by sectioning the whole alimentary canal of the Termes, hoping in this way to obtain some sections of Trichonympha in a direction favorable for settling this point. I was not disappointed.

To my astonishment I found that the small intestine was completely packed with animalcules, and among them hundreds of Trichonympha; these, however, were not promiscuously distributed through the parasitic mass, but were, as a rule, excluded from the periphery of the intestine. This position, of course, precluded the possibility of their attaching themselves directly to the wall of the host's intestine.

The sections of Trichonympha thus obtained revealed absolutely no trace of such an oral aperture as that described by Kent. They did show, however, an interesting condition of affairs, which I think may perhaps account for the presence of the numerous fragments of ligneous fibre and other food particles so often found within the body, without necessarily supposing them to have entered through a persistent mouth. In many of the cross sections of the posterior half of Trichonympha I observed deep folds of the body wall; these almost invariably contained cilia, doubtless engulfed at the time of the folding (Plate **2**, Figs. 9, 10, and 14). Particles of wood fibre were also seen entangled among the cilia in these folds (Fig. 10, *fbr. lig.*). I think we have in this condition an explanation of the mystery. Cilia entangling particles of woody fibre become surrounded by a deep fold of the posterior part of the body. The most of the cilia are probably afterwards withdrawn from the fold, but the lips of the fold become so closely applied to each other (Fig. 14), that the ligneous particles are left behind in the depths of the fold. I believe that the lips of the fold afterwards fuse together, that the walls of the infolded portion then disappear, and that the food thus finally becomes entirely enclosed in the body protoplasm of the parasite. The condition of the body wall at α in Figure 14 seems to indicate that the wall is there in process of disintegration or dissolution.

This is certainly a remarkable method of feeding for a ciliate infusorian; but I see no escape from the conclusion that solid food material never enters the animal in any part of the anterior nucleus-containing portion of the body; for of the hundreds of specimens that I have examined, both living and dead, none have ever shown solid particles of food in the anterior region, whereas the absence of ligneous matter from the posterior part of the body is a condition rarely met with. It seems highly improbable — to say nothing of the absence of any trace of a permanent oral structure — that solid food should pass through this anterior region so quickly that not a single case of its passage, or of its presence in this part, should have been discovered by any one of those who have studied these parasites.[1] But besides this, it is to be noted that the wall of the whole posterior part of the body is thin and exceedingly delicate, so that it would not present any great barrier to the entrance of foreign particles. It disintegrates so readily that I have seen this portion of a living animal go to pieces completely and disappear, while the anterior half, bearing the cilia, continued to swim around.

For the sake of convenience in description, I shall recognize in Trichonympha three regions (compare Plate **2**, Figs. 13, 15, 7): first, an anterior nipple-like part, which is quite sharply separated from the following region; secondly, the middle or bell-shaped part, the axial hinder portion of which usually projects a greater or less distance into the following or third part, and always contains the nucleus. These two parts together have been called by Leidy the " head." Thirdly, the posterior part, to which Leidy gave the name of " body."

---

[1] It is true that Kent speaks of seeing the "pharynx" and digestive cavity densely packed with milk corpuscles; but while this is the case in the posterior portion of the body, I have never seen milk globules or other particles of food in any part of the organism that could be likened to a pharynx.

Frenzel ('91) likewise was unable to find direct evidence of the existence of a mouth opening in Leidyonella. Although he inclined to the opinion that it was located at the anterior end of the elongated neck-like region, he admitted the possibility that it might be located elsewhere. Grassi ('85), too, was equally unsuccessful in locating the mouth in Joenia, although in this genus likewise the presence of particles of woody fibre in the body shows that solid food is taken in.

I begin with the anterior region, which I have found to be of rather complicated structure. To aid in the description, I have made several large semi-diagrammatic sketches (Plate **2**, Figs. 7, 8, 11, 12, 17). Figures 7 and 8 are intended to represent sections not thicker than the space between two successive longitudinal rows of cilia.

The *nipple-like part* of Trichonympha is, as the name which I have given it implies, a conical, more or less elongated protuberance at the front end of the parasite. According to its state of contraction it is one half, two thirds, or even more than two thirds, as thick at its base as it is long. The anterior end is evenly rounded or sometimes more pointed. Seen in profile its outline at the posterior end usually passes gradually into that of the middle part, but at times it appears sharply separated from this part by a deep constriction. Deep focusing and especially longitudinal sections show that the separation is more complete than superficial focusing would lead one to suppose.

The " nipple " consists of a cylindrical, or slightly tapering, rod-like axis (Plate **2**, Figs. 7, 8, 18, *ax.*), composed of finely granular protoplasm, and one or more enveloping layers unlike in structure. The anterior end of the axial rod is expanded into a knob-like enlargement (Figs. 7, 8, *tub.*), the anterior surface of which has a conical (Fig. 7), or more commonly a hemispherical (Fig. 8) form. The rod is narrowest a little in front of its middle, and thence increases in thickness very gradually both toward the knob and toward the " bell." The protoplasm of the axial rod is continuous behind with the granular protoplasm which occupies the axis of the " bell," and its surface appears to be differentiated into a thin membrane. This protoplasmic axial rod is surrounded by two, and possibly sometimes by three, well differentiated layers of formed substance (Fig. 7, *st.′*, *st.‴*; Fig. 8, *st.′*, *st.″*, *st.‴*). The middle layer often appears as though caused by an accidental separation between the outer and inner layers, but it is of so common occurrence that I do not feel able to declare positively that it is merely an artificially produced space.

The anterior extremity of Trichonympha terminates in a colorless translucent cuticular cap (Figs. 7, 8, *pil.*), which stains only slightly at most, and frequently not at all. The centre of the cap covers the anterior expanded end (*tub.*) of the rod-like protoplasmic core, and its margin rests on the anterior sloping surface of the outer layer (*st.'''*), while the anterior end of the inner layer (*st.'*) is covered by the expanded knob-like portion (*tub.*) of the protoplasmic core (Figs. 7 and 8).

The whole of this portion, forming the nipple-like projection of the anterior extremity of the animal, is very active in the living creature; it is constantly in motion, turning from side to side, and, as it were, nosing its way through the crowd of its associates.

The axial rod (Figs. 7, 8, *ax.*) is apparently the only means of union between this nipple-like part of the animal and the bell-shaped region, for a fissure (Figs. 7, 8, *fis.*), encircling the base of the nipple, penetrates the layers surrounding the axis, thus severing all other connection. Behind the fissure, what seem to be continuations of the outer and inner layers of the nipple are carried backward over the bell-shaped region, i. e. over a little less than one third the length of the animal. A middle layer never appears in this region, a fact which makes it seem probable that such an appearance in the nipple region is due merely to a space between the inner and outer layers. Since the enveloping layers are so much alike in the nipple- and bell-shaped regions, I shall not attempt to give a separate description of them in each region, but proceed at once to state what I have to say about these layers for the whole "head" region.

The inner layer stains only slightly, if at all. From the fissure backwards, as far as it extends, it is marked by fine lines perpendicular to the surface. This appearance is due to the cilia, which penetrate both the enveloping layers. The same structural condition probably exists in front of the fissure, although it was not possible, owing to the small diameter of the nipple-like projection (about 6 μ) and the thickness of my sections (3.3 μ), to detect any striations.

The cilia arise from the granular protoplasm, at the deep surface of the inner layer, which they traverse, and thus give a striated appearance (Fig. 16, *st. str.*). They are of about the same refractive power and stainability as the outer layer, and consequently I have not been able to trace them through that layer; but I think that their passing through it is hardly questionable. The arrangement of the radial striations of the inner layer, which I believe to be due to the cilia, is best made out from tangential sections of the bell, where their cut ends appear as dots. The dots are placed in quincunx order, much as shown in Fig. 20. This arrangement gives two series of diagonal rows of dots crossing each other nearly at right angles and making angles of 45 degrees with the longitudinal axis of the animal. Secondary rows, both parallel and perpendicular to the longitudinal axis, though less regular than the oblique ones, are easily recognizable. Owing to the surface of the bell being curved, the arrangement in quincunx is not as evident as I have represented it diagrammatically in Figure 20, but has more the appearance shown in Figure 19, where the oblique and transverse rows are somewhat curved, and the longitudinal ones diverge slightly as they pass backwards.

The outer layer (Fig. 7, *st.'''*) is composed of a series of ridges, or, more properly speaking, plates. These plates, cut crosswise, are shown in Figure 16 (*st.'''*), which represents a transverse section through the middle of the bell-shaped ciliated portion of the body, about in the place indicated by the line 16–16 in Figure 15. The plates are seen more clearly in the diagrammatic cross section shown in Figure 17, *st.'''*. In surface views of the animal each of the plates of the nipple appears to be split into two at the region of the fissure (Fig. 11, *fis.*); this, however, is only an optical illusion. Although the plates of the bell-shaped part are twice as numerous as those of the nipple-like part, there is no continuity between the two sets, the appearance of splitting being due to the overlapping of the anterior set over the posterior one. The nature of this overlapping (Fig. 12, *fis.*) may be seen in optical longitudinal sections. The plates of the outer layer coincide with the longitudinal rows of cilia. Their inner edges are slightly serrated (Fig. 8, *csp.*), owing to a slight inward prolongation of the plate wherever a cilium in passing through meets it. It is this condition which causes the interrupted appearance of the plates seen in tangential sections (Fig. 20, *csp.*).

The *bell-shaped region* is generally sharply marked off from the anterior or nipple-like part by a deep constriction (Plate **1**, Figs. 1–6); but sometimes there is a more gradual transition (Plate **2**, Figs. 7, 8). The boundary between the "bell" and the "body" is ordinarily marked by a deep constriction (Plate **1**, Figs. 1, 6), or a shoulder-like projection of the "body" beyond the outline of the "bell" (Plate **2**, Figs. 7, 15). The place of this constriction may for convenience be called the lip of the bell, though the pendant central mass of the protoplasm of the bell containing the nucleus often projects far behind this rim or lip. When the animal is at rest, the bell is of fairly regular and symmetrical form (Figs. 13, 15), but the extreme mobility of the whole head region causes it when in action to take a great variety of shapes (Plate **1**, Figs. 1–6).

The protoplasm of the bell is differentiated into two distinct kinds, a coarser and a finer. The coarsely granular protoplasm is situated chiefly in the anterior portion of the bell (Fig. 7, *pr'pl.*), but it is also continued backward along the surface, and likewise forms a pendant-like structure in the axis of the bell (*pr'pl. ax.*, Figs. 7, 13, 15). It stains a little darker than the finer protoplasm which occupies the rest of the bell, but the transition between the two kinds is not very abrupt.

Extending backward from the lip of the bell is a coarsely granular protoplasmic partition (Fig. 7, *st. gran.*), continuous with the coarsely granular protoplasm of the surface of the bell, and marking the boundary between the "head" and the "body" of the animal. It has the form of a hemispherical bowl, at or near the bottom of which is situated the nucleus. Although I have been unable to discover in connection with this granular partition the existence of any fine membrane serving to completely separate head and body, yet the constant relation of the nucleus to this granular layer proves the latter to be substantially a permanent boundary between these two regions of the animal. In cross sections of the animal in the region of the nucleus (Figs. 21, 23; compare the position of the lines 21–21 and 23–23 in Fig. 15), this partition gives rise to a kind of radiation, which seems to emanate from the nucleus. This appearance might be produced if the bowl-shaped layer of granulations were corrugated or thrown into radiating folds; but I believe it is due instead to a regular alternation in the *thickness* of radiating portions of the bowl. As seen in cross sections (Figs. 21, 23) this bears a slight resemblance to the crown of rods (bastoncelli) figured and described by Grassi ('85, p. 236, Figs. 1, 2, 6), as nearly enveloping the nucleus in the case of Joenia annectens; but the fact that the bastoncelli have a more precise form, being short club-shaped and curved, as well as the fact of their not being limited to a single zone, seems to me to preclude the possibility that these two structures are homologous.

The nucleus (Fig. 7, *nl.*) is situated in the anterior or "head" portion of the animal, a little posterior to the constriction at the surface which marks the transition from the "bell" to the "body." It lies wholly within the bell-shaped portion, however, and is generally surrounded by a thin sharply defined nuclear membrane. I have almost invariably found the chromatin broken up into chromosomes of varying size and shape, and without definite arrangement.

Very frequently the nucleus is invested with an immensely thickened membrane (Plate **2**, Fig. 22). This nuclear envelope consists of a clear homogeneous substance, which stains in eosin, but not in hæmatoxylin.

I have found several stages which I believe lead up to this condition. Apparently the substance which is destined to envelop the nucleus first collects along the partition separating the body from the head of the animal (Fig. 13). Possibly the formation of this thick envelope is preparatory to the production of the spores.

The posterior or body half of the animal is principally occupied by a highly vacuolated protoplasmic mass (Fig. 7), which has usually reached the state of a coarse reticulum. In this reticulum large pieces of wood fibre and spores of fungi are frequently found embedded. This central protoplasmic reticulum is completely surrounded by a granular protoplasmic wall (*st. gran.'*, Figs. 7, 13, 15), which is continuous in front with the granular partition separating the "head" from the "body."

The granular wall is not very thick, and passes on its inner surface rather gradually into the protoplasmic network; but it is more sharply defined on its outer surface, though even here the transition to a rather thick cortical layer (*st. ctx.*, Figs. 7, 13, 15) immediately outside it is not very abrupt. This cortical layer is composed of finely granular almost homogeneous protoplasm, and is of nearly, though not quite, uniform thickness. Its average thickness is about the same as that of the inner layer enveloping the bell.

The surface of the "body" appears to be traversed by nearly equidistant lines, which have a slightly spiral — left-handed or læotropic — course (Plate **1**, Figs. 1, 2). These lines appear to be continuous in direction with the innermost set of cilia, which cross one another at the posterior tip of the body, and in fact the lines are in my opinion due exclusively to the presence of these cilia, which are closely applied to, but are entirely free from, the wall of the "body." Frenzel's description of the condition in Leidyonella is certainly not applicable here. Frenzel ('85, pp. 306, 307) maintains that in Leidyonella the rigid cilia arise at or near the anterior end of the body, but that, instead of being free throughout their whole length, they are fused with the peculiar cuticula which covers the body, causing ridges, which have a slightly spiral course (he does not say whether right or left, and his figures are noncommittal), and that they become free only as they project beyond the posterior extremity of the body. These ridges are stated to be much more prominent in the anterior than in the posterior part of their course. But, whatever may be the condition in Leidyonella, the spiral markings in Trichonympha are not traceable forward any further than the boundary between "body" and "bell," and they are not due to confluence of cilia with the wall of the body of the parasite.

The questions of reproduction and development in Trichonympha, though interesting, are very difficult, and I shall not be able to say much on them.

I have chanced upon three individuals, which I at first thought to be stages of division (Plate **3**, Figs. 24–26), but having seen only these three, and these being all from the same host, I am now inclined to think that they are simply abnormal forms. But whether these are normal or abnormal, I believe that division must be of rare occurrence.

Leidy has figured several forms (Plate 51, Figs. 11–20), always found associated with Trichonympha, which he thinks may be their young; but I believe that not all the forms referred by Leidy to Trichonympha can be the young of that genus. Perhaps, indeed, none of them are. Those which seem to me to present the best evidence of being the young of Trichonympha are shown in Plate **3**, Figs. 27–29 (compare also Leidy's Plate 51, Fig. 11). These individuals possess a nucleus situated in about the same relative position as that of the adult Trichonympha, and are provided with long cilia. The cilia begin at the base of a smooth knob (Fig. 29), with which the anterior end of the animal terminates, and follow from there the course of deep spiral grooves that have the direction of the threads of a right-hand screw, not, as one might infer from Leidy's Figure 11, that of a left-hand screw. The grooves are much closer together on the anterior than on the posterior portion of the parasite, and consequently, as in the adult Trichonympha, the cilia are much concentrated into this region. Again, as in the adult Trichonympha, a bunch of long cilia trails out behind the parasites of this type. Moreover, the anterior cilia alone are used, as in the adult Trichonympha, for locomotion, the body often remaining during locomotion perfectly rigid and the posterior cilia quiet.

This spring (1896) I have noticed a great many specimens of this parasite with a very much enlarged, apparently swollen, anterior knob (Fig. 28); but what this condition signifies I have been unable to determine.

Notwithstanding these several points of agreement, there seem to me to be almost insuperable obstacles to assuming that there is a genetic relation between the two forms. Chief among these is the pronounced dexiotropic course of the spiral groove and accompanying bands of cilia in the supposed young; whereas in the adult Trichonympha the bands are *longitudinal* and are limited to the anterior or bell-shaped part. A direct conversion of one of these conditions into the other seems to me highly improbable, while the obliteration of one and a substitution of the other would amount to nothing less than a metamorphosis, none of the steps in which have been observed.

Another point of difficulty is the entire absence in the supposed young of any partition separating the nucleus-bearing anterior portion of the organism from the posterior portion.

The other forms, resembling those which Leidy thinks may also be young of Triconymphæ, I have represented in Figures 30–32, 35–39, and 42–44. I can see no sufficient reason, however, for supposing them to be young Trichonymphæ. The nucleus of these forms is situated at the extreme anterior end of the body. The anterior tip terminates in a rounded projection, but it has not the form of the knob seen in Figures 27 and 29, and a comparison with the cap seen in adult Trichonymphæ is more difficult in this case than in that of the forms last described. The cilia are of very nearly equal length over the entire body. They are arranged in bands running spirally around the animal, and the spirals run in the same direction (dexiotropic) as in the forms we have just been discussing.

There are, however, so many points of difference between these two kinds of supposed young parasites as to render it probable that they are not connected with each other genetically any more than they are with Trichonympha. It will be observed not only that the nuclei are differently situated in the two forms, but also that in those shown in Figures 30–32 and 35–38 the interval between successive bands of cilia remains nearly constant throughout the entire length of the animal, quite unlike the condition obtaining in the other forms.

This form is also found in a great variety of sizes (Figs. 30, 31, 35), the largest being considerably larger than the individuals of the other form represented in Figures 27 and 28. The shape of the animal is characteristic, being in the living condition long and slim. Figures 37, 39, and 42–44 represent living specimens. Figure 38 shows one that died in normal salt solution. Figures 30–32, 35, and 36 represent the shapes they assume when killed with corrosive sublimate. Their method of locomotion also serves to distinguish them from the forms which I have last described, for they often move, independently of ciliary activity, by changes in the form of the whole body (Figs. 39, 42, 44), — sometimes with the wriggling, squirming motion of a worm, at others, swelling out in places to almost double their average diameter, and then slowly contracting their body-wall (Fig. 44), they produce a kind of peristaltic motion, which may aid in locomotion. The smaller ones (Fig. 43), when travelling very rapidly in a straight line, revolve around the longitudinal axis, their bodies changing form little or not at all. This rotation is undoubtedly due to the spiral arrangement of the cilia, but the constant motion of these organs makes it impossible to discover in living specimens what the arrangement of the cilia is.

The bodies of these worm-like animalcules (Figs. 30–32, 37–39, 42–44) are invariably filled with great numbers of large protoplasmic granules; this is not the case with any of the other parasites.

It seems to me that the characters of this form are sufficiently definite and different from those of the other forms described to allow one to consider them the representatives of another species.

2. Pyrsonympha vertens.

Plate 3, Figs. 33, 34, 40, 41; Plate 4; Plate 5.

Pyrsonympha in its mature state is much larger than Trichonympha. Either the parasites found in the vicinity of Cambridge attain a greater size than those studied by Leidy, or else this author failed to see the largest individuals, for the longest specimen seen by Leidy measured only 160 μ, whereas the one which is shown in longitudinal section in Figure 33 (Plate **3**) is 275 μ long, exclusive of the peduncle; this being a large, but not an exceptionally large individual.

Pyrsonympha, like Trichonympha, evidently feeds on solid food, so that the question again confronts us, How does this food enter the body? Sometimes the whole posterior portion of the animalcule is filled with fragments of wood fibre (Fig. 34). These fragments are often of considerable size. I have seen, within the posterior part of the body, a single rectangular piece so large that it touched both sides of the body, and extended anteriorly almost to the nucleus. Surely, a mouth large enough to swallow such a portion of food must be recognizable; but I have been unable to discover any aperture whatsoever in the body-wall of the animal.

Pyrsonympha is usually more or less club-shaped, the relative proportions of length and thickness, and the particular form, being of course dependent on the degree and nature of its contraction (Plate **3**, Figs. 33, 34, 40, 41; Plate **4**, Figs. 45, 51, 53, 55). In the adult condition it appears always to be attached to the wall of the host's intestine, a fact which Leidy, strangely enough, seems to have entirely overlooked. The attachment is by means of the narrower end, which is prolonged into a sort of homogeneous stalk or peduncle, having only a slender connection with the main portion of the parasite. The peduncle is from 1 μ to 1.5 μ in diameter, and may attain a length of at least 75 μ. It is deeply embedded in the epithelial wall of the host's intestine. I am not certain that I have been able to trace it to its end, and do not know if there is any specialized structure at the end; consequently I cannot state the possible maximum length. It is usually of almost uniform calibre throughout the most of its length. The region near the point of attachment, however, often shows a spindle-shaped enlargement (Plate **4**, Fig. 45). There is invariably a spheroidal structure that I have called the knob or tubercle (Figs. 46, 47, *tub.*), which serves as a means of connecting the peduncle with the rest of the body; when an artificial separation between body and peduncle takes place, the tubercle may remain attached to either part, but it usually separates from the body (compare, however, Fig. 47). The tubercle is somewhat thicker, and becomes much more deeply stained, than the peduncle; it is homogeneous and highly refractive.

The attached end of Pyrsonympha is that which Leidy has called the anterior end. Accepting this designation simply as a convenience in description, it may be said that the free posterior part of the parasite projects with a rounded end into the lumen of the host's intestine. The body of the parasite, from the narrow tuberculate part to the free rounded end, looks like a thin sac.

The body-wall itself is frequently excessively thin, and in places the body seems to be almost naked and amœboid in its nature. The slightest pressure of an object on its surface would cause it to enter the substance of the body. I believe that something of this kind is represented in Figure 40 (Plate **3**); at any rate, in this case a particle of wood fibre was found about three fourths engulfed by the animal; whether the fragment was accidentally forced into the body, or whether the animal was taken in the act of ingesting it for food, I am unable to say. The parasites, of which this was one, had been removed from the host for about an hour when I discovered this individual. During the three or four minutes that I watched this one no change took place, and at the end of that time it was dead. So it is still only a matter of conjecture that Pyrsonympha engulfs its food by the exceedingly mobile posterior portion of the body.

However that may be, the body-wall is so thin in all regions as to make the condition noteworthy. There is no place where its thickness is sufficient to allow it to be readily measured. In fully grown individuals the body is only sparsely covered with cilia, and portions of the surface seem to be entirely destitute of them. When present they are scattered irregularly, apparently without relation to the contractile cords of the body-wall. The young, as we shall see later, are provided with a coat of abundant cilia uniformly distributed.

The body-wall is not without further differentiation, for at regular intervals it is marked by darker lines, which have the appearance of thickenings of the wall, or of separate cord-like structures applied to its inner surface. These are really contractile cords, which arise at the knob-like structure of the anterior tip of the parasite where it joins the peduncle. These cords are usually grouped together at the anterior end of the body, so that a portion of the surface is quite bare of them (Plate **4**, Fig. 51 *a*). They pass backward in a slightly spiral direction (læotropic), leaving between one another equal spaces. As a rule, each cord can be traced to the posterior extremity of the animal, and thence back again on the opposite side of the animal to the anterior end; but sometimes the cords apparently terminate in cup-like depressions in the body-wall, which resemble pock-marks, being outlined by coarse granular protoplasmic rings (Fig. 51, *ann.*). The cords are frequently so superficial that in profile views of the animalcule they are seen to cause the surface to project in the form of ridges. In some individuals there is to be seen in the middle of the space between two successive cords another and much finer line (Plate **4**, Figs. 47, 54) running parallel with them. This narrower line or cord is apparently embedded in a more or less clear homogeneous substance, while the larger cords are surrounded by coarse granular protoplasm. In other cases the larger cords occupy the clear areas, and midway between them are sharply marked lines of coarsely granular protoplasm, which stains more deeply than the rest of the protoplasm (Fig. 51).

In living specimens these cords keep up an incessant undulatory motion, producing an effect which very closely resembles bands of vibrating cilia The body of the adult, however, is generally quite bare of cilia, but when it is ciliated, the cilia are, as I have said, scattered promiscuously over the body, irrespective of the contractile cords.

The contents of the sac-like body are finely and rather uniformly granular, and not very thick or viscid, and there are appearances of vacuolation in them.

The nucleus of Pyrsonympha is a large pear-shaped or sometimes oval body, generally situated at about one fourth or one third of the distance from the anterior or attached end to the posterior end, and its more pointed extremity is turned toward the attached end of the animalcule. It always contains a nucleolus (Plate **4**, Fig. 47, *nll.*) at its larger end, and frequently it is highly vacuolated at its anterior end. Figure 52 (Plate **4**) represents a cross section of a Pyrsonympha through the nucleus, showing its position and that of the flagellum (*fg.*) in relation to the wall of the body. The nucleus varies considerably in shape; sometimes it is very much attenuated (Fig. 50), and at others almost spherical (Fig. 53, *nl.*).

Within Pyrsonympha is a lash-like filament or flagellum (*fg.*), as I shall call it, which is by far the most remarkable structure of this parasite. In the living specimen it is in constant motion, great waves passing from the attached to the opposite end of the animal, often giving it the appearance of a revolving polygon inside the animal. Leidy says, "The motion of the undulating cord and of the animal together impressed me with the idea of a snake in a bag, making its presence obvious in active contortions." The effect of this flagellum is not unlike that of a churn, for it keeps the contents of the sac-like body, including the food, thoroughly stirred up.

The flagellum is of nearly uniform thickness throughout the most of its length, and, as cross sections (Fig. 52) show, is oval in section; its diameter varies with the state of contraction, but averages about 1.5 μ by 2 μ. Near its anterior end, where it joins the peduncle by means of the darkly staining tubercle, it sometimes becomes very much attenuated (Plate **4**, Fig. 46). I am not certain, however, but that this may be due to abnormal tension induced by the increased activity of the flagellum when the parasite is put in normal salt solution. However this may be, the posterior portion of the flagellum tapers off very gradually, finally becoming very fine at its posterior end (Figs. 45, 53, 55).

Throughout the most of its length it is quite free from the body-wall, and moves about with vigorous strokes in the most unexpected manner. It is, however, attached to the body-wall at or near the posterior end of the parasite, as well as at the region of the peduncle. But quite frequently it seems to break loose from this posterior place of attachment, — perhaps owing to a too violent whipping about caused by the stimulating effect of the salt solution, — and then it sometimes projects posteriorly in the form of a tail-like appendage. This caudal appendage is surrounded by a layer of protoplasm, which has considerable thickness at its base, but becomes reduced to a condition of great tenuity (Plate **3**, Fig. 34) at its tip. It flaps backward and forward very violently with every undulation of the flagellum.

Leidy ('77, p. 437) says of Pyrsonympha, "Sometimes too it appears terminated by a caudal appendage of variable form and length, but this has seemed to me to be a production resulting from change due to dissolution." It does not appear from anything said elsewhere, or from his drawings, that he connected the presence of this caudal appendage with the vibrating cord.

The method employed in removing from the host the living animalcules for study has proved to be important, for it is to this that I owe the discovery of the peduncle previously described. Leidy speaks of gently pressing the intestine of the host, and thus forcing out the parasites. Instead of doing this, I removed the intestine into normal salt solution and on the slide teased it into pieces with needles. In this way of course many fragments of the intestine were found mingled with the parasites. These were frequently covered with Pyrsonymphæ, so closely packed together that they looked at first sight like large epithelial cells. Each of the parasites was attached to the fragment of the intestinal wall by a long filament (Plate **4**, Fig. 45). I think that Leidy saw this filament or peduncle, as I have already called it, for he says ('77, p. 438), "In the process of dissolution of the animal, the undulating cord [flagellum] often appears to project to a variable extent from the narrower end of the body"; but he did not recognize that this projecting part was a means of attachment, for on forcing Pyrsonymphæ from the intestine the most of this peduncle must invariably have been broken off. Normally, I believe, all mature Pyrsonymphæ are attached to the intestine by means of this peduncle.

The few evidences of reproduction which I have observed relate to the conditions of the nucleus or the size of the individuals. I have observed nuclei in what I believe to be various stages of division (Plate **4**, Figs. 48, 49, 55). This shows that probably reproduction by division takes place occasionally. Perhaps Figure 53 represents an individual recently formed in this way; the presence of the nucleus in the posterior portion of the parasite certainly points to that conclusion. Individuals produced by the division of a large adult Pyrsonympha should of course resemble the adult form in the almost total absence of cilia, and also in the possession of a flagellum. It therefore seems safe to assume that almost all unusually small Pyrsonymphæ possessing these qualities (Plate **5**, Figs. 62, 64) were recently formed by division.

Besides young of this type, there are found swarms of immature Pyrsonymphæ with essentially different characteristics. These are, for example, profusely covered with fine, short cilia of nearly equal length (Plate **5**, Figs. 58, 61, 63). Apparently, the flagellum is frequently wanting in these forms, or at least cannot be distinguished (Figs. 57, 63). The superficial muscular cords exist, but take a longitudinal course as often as a spiral one (Figs. 57, 61). Sometimes they are distributed over only a part of the animal (Fig. 61). The nucleus of these small individuals resembles that of the adult, but is situated at the extreme anterior end. If, therefore, it were not for the presence of the flagellum and peduncle in some of these forms, we should be quite unwarranted in supposing them to be in any way related to Pyrsonympha. As it is, however, I think there can be no doubt of the relationship. The flagellum and peduncle are both absent in some forms (Figs. 59, 60, 65) which I take to be the earliest known conditions of this parasite.

I have come to the conclusion that the flagellum of Pyrsonympha is merely a differentiation of one of the superficial muscular cords. We may conceive that the cord which is destined to become a flagellum, after becoming larger, stronger, and more active than any of the other cords (Plate **5**, Fig. 61), simply splits off from the inner surface of the body-wall, remaining fixed only at its two extremities; thus it enjoys free play for all its peculiar undulations.

The peduncle is apparently a slow-growing structure. In sections of the intestine one often finds young parasites in closely packed masses, lining considerable portions of the intestinal wall (Plate **5**, Fig. 56). Their anterior ends lie very close to the intestinal epithelium, thus showing that the peduncle is still very short. The young here referred to (Plate **5**, Fig. 56) are not more than one third or one fourth as long as the adult parasites shown in Figure 45 (Plate **4**). The deeply stained body which is to be seen at the anterior tip of even the youngest individuals (Fig. 56) is the knob-like structure or tubercle of the adult, from which the peduncle arises.

In their activity the young far exceed the adults, for besides the undulation of the muscular cords, the animal is constantly changing its shape. Figures 59, 60, and 65 (Plate **5**) represent different shapes, taken by the same individual in the course of a few minutes.

It is of interest in this connection to note the effect of these parasites on the intestine of the host (Plate **5**, Fig. 56). The epithelial lining is very much indented. The peduncles force their way between the cells, reaching sometimes almost to the underlying muscular layer. The cells themselves are often reduced in size, but otherwise apparently perfectly healthy. It is a mystery how the host can support such a vast number of parasites, unless they in turn are in some way of benefit to it.

3. Dinenympha gracilis.

Plate 6, Figures 66–72.

I have found it almost impossible to draw any sharp line of distinction between Dynenympha and the young of Pyrsonympha; in fact I doubt very much whether Dinenympha should be considered as anything else than a very early stage of a developing Pyrsonympha.

Dinenympha never possesses a flagellum or a peduncle, although at the anterior tip of the animal there is frequently a deeply stained body resembling the tubercle of Pyrsonympha. The body of Dinenympha is long and slim, slightly flattened on one side, and generally twisted with one or two dexiotropic turns. Running parallel with this twist, but upon the convex side only, there are from seven to nine muscular cords, resembling those of Pyrsonympha; but they often cause the surface to project much farther than is usual in Pyrsonympha, giving the animal a fluted appearance. This is shown in Figures 69 and 70 (Plate **6**), which represent the upper and lower surfaces respectively of the same individual. Similar views of another individual are shown in Figures 71 and 72.

The animal is generally almost devoid of cilia, except for a tuft at the posterior end (Figs. 67, 68), or occasionally a few cilia at both extremities (Figs. 66, 69). Sometimes, however, it is thinly ciliated all over (Fig. 72). I think Leidy must have mistaken the undulatory motion of the muscular cords for the vibration of bands of cilia, for I have found that individuals with abundant cilia are rare.

The nucleus is situated near the anterior extremity of the parasite; it is oval and homogeneous, or finely granular, and sometimes (Fig. 66) shows a single darker structure like a nucleolus. The nucleus varies in size from $9 \times 5.5\,\mu$ to $5.5 \times 3.6\,\mu$.

The motions of the living Dinenympha are exceedingly interesting, but Leidy has amply described them.

Dinenympha, like its companion parasites, lives on solid food; but it possesses no discoverable oral aperture.

4. Gregarinida.

Plate 6, Figs. 73–76.

Leidy ('81, p. 441) speaks of having only once noticed a small Gregarine among the other parasites of Termes. I have, however, found Gregarines very common in some hosts. They are found, almost without exception, in the anterior portion of the small intestine only. Sections through this part often reveal great numbers of cysts (Plate **6**, Fig. 75). They belong to the Polycystidea. Figure 73 (Plate **6**) shows a very characteristic appearance of a living specimen, and Figure 74 that of one filled with sporocysts.

In sections (Fig. 76) the protomerite (*pr'mer.*) is seen to be compactly filled with protoplasm, the anterior half of which stains more deeply than the rest. The posterior half appears to be made up of globules somewhat flattened by mutual pressure. In living specimens the anterior portion of the protomerite is quite transparent, being free of all coarse granules (Fig. 73).

The deutomerite (Fig. 76, *deu'mer.*) is generally only loosely filled with a coarse protoplasmic network. It contains the large, round nucleus, generally situated quite centrally. Within the nucleus is always to be found a single large deeply stainable nucleolus.

In conclusion, I wish to express my very deep indebtedness to Dr. Mark for whatever there may be of value in this paper. The work was taken up at his suggestion, and carried on under his very kind and careful supervision.

Cambridge, May 12, 1896.

PAPERS CITED.

Frenzel, J.
'91. Leidyonella cordubensis nov. gen., nov. spec. Eine neue Trichonymphide. Arch. f. mikr. Anat., Bd. XXXVIII. pp. 301–316. 4 Fig.

Grassi, B.
'85. Intorno ad alcuni protozoi parassiti delle Termiti. (Nota letta 15 Gennaro 1885.) Atti dell' Accad. Gioenia Sci. Nat. in Catania, ser. 3, Tom. XVIII. pp. 235–240. 7 Fig.

Kent, W. S.
'85. Notes on the Infusorial Parasites of the Tasmanian White Ant. (Read Nov. 17, 1884.) Papers and Proceed. Roy. Soc. Tasmania for 1884, pp. 270–273. *Reprinted in* Ann. & Mag. Nat. Hist., ser. 5, Vol. XV. No. 90, June, 1885, pp. 450–453.

Leidy, J.
'77. On Intestinal Parasites of Termes flavipes. Proceed. Acad. Nat. Sci. Philadelphia, 1877, pp. 146–149. (Read Apr. 17; printed June 26.)

Leidy, J.
'81. The Parasites of the Termites. Journ. Acad. Nat. Sci. Philadelphia, New (Second) Series, Vol. VIII. Part 4, (1881,) pp. 425–447.

Lespès, C.
'56. Recherches sur l'organisation et les mœurs du Termite lucifuge. Ann. Sci. Nat., sér. 4, Zool., Tom. V. pp. 227–282.

EXPLANATION OF PLATES.

All the figures, with the exception of those of Plate 2, were outlined with the aid of an Abbé camera lucida.

The high magnifications were obtained mostly by the use of a Zeiss 1.5 mm. apochromatic homogeneous immersion objective with No. 4 compensating ocular.

LIST OF ABBREVIATIONS.

ann.	Ring of protoplasmic granules.
ax.	Cylindrical axis of the "nipple" in Trichonympha.
cil.	Cilia.
csp.	Tooth-like processes of the inner surface of the outer layer of the "bell."
deu'mer.	Deutomerite.
fbr. lig.	Wood fibre.
fg.	Flagellum.
fis.	Fissure.
mu.	Muscle.
nl.	Nucleus.
nll.	Nucleolus.
pd.	Peduncle.
pil.	Cap.
pli.	Fold.
pr'mer.	Protomerite.
pr'pl.	Coarsely granular protoplasm of "bell."
pr'pl'.	Finely granular protoplasm, making up most of the contents of the "bell."
pr'pl. ax.	Protoplasm situated in longitudinal axis of the bell of Trichonympha, which is coarser and more deeply stained than the surrounding protoplasm.
spo.	Spores of a fungus.
st.'	Inner layer of "nipple" and "bell" of Trichonympha.
st.''	Middle layer of same.
st.'''	Outer layer of same.
st. ctx.	Cortical layer of granular protoplasm.
st. gran.	The granular protoplasmic layer separating the "bell" from the posterior part (body) of Trichonympha.
st. gran.'	Granular protoplasm marking the region of transition from the superficial (ectosarc) to central (entosarc) portion of the protoplasm in the posterior half ("body") of Trichonympha.
st. str.	Striated layer of the "bell" of Trichonympha.
tub.	Knob-like enlargement of the anterior end of the protoplasmic axis of the "nipple," Trichonympha. Also knob-like structure at the anterior extremity of Pyrsonympha.

PLATE 1.

All figures are of Trichonympha agilis.

Figs. 1, 2. Normal appearance of parasite when examined in diluted albumen. × 520.

Fig. 3. Appearance of anterior tip of Trichonympha viewed from in front.

Figs. 4–6. Animals in diluted milk, showing corpuscles seized upon by the long rigid cilia and dragged after the animal. × 520.

[illegible] PLATE I

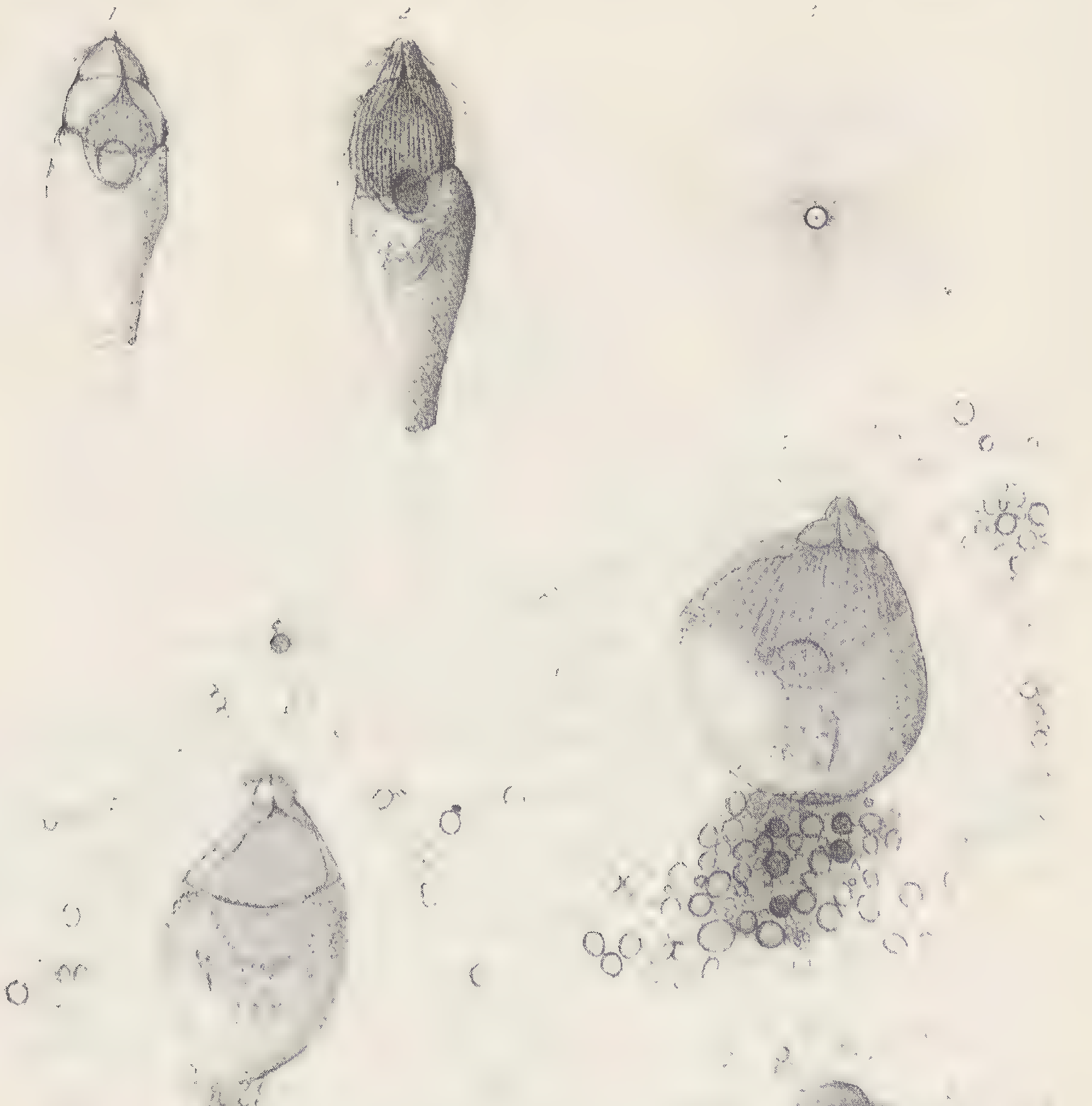


PLATE 2.

All figures are of Trichonympha agilis.

Fig. 7.	Diagrammatic longitudinal section through the anterior portion of Trichonympha, imagined to be not thicker than one band of cilia.
Fig. 8.	Same as Figure 7, but showing an additional layer (*st.''*) in the nipple-like anterior extremity.
Fig. 9.	Cross section through posterior portion or "body," showing a fold in the body-wall, in which cilia have been engulfed.
Fig. 10.	Section similar to that of Figure 9, except that particles of wood fibre are entangled with the cilia in the engulfed portion. *spo.* Spores of Fungi eaten by the animal.
Fig. 11.	Diagram of a portion of the surface of the anterior end, the "nipple," and part of the "bell."
Fig. 12.	Diagram of side view of same region as that shown in Figure 11.
Fig. 13.	Complete longitudinal section, showing a gathering of a clear protoplasmic substance about the nucleus; probably an early stage in the development of an immensely thickened nuclear membrane such as is shown in Figure 22.
Fig. 14.	Cross section of posterior portion, showing a fold, as in Figures 9 and 10, the walls of which are beginning at *a* to disintegrate.
Fig. 15.	Complete longitudinal section of an individual more shortened than that of Figure 13.
Fig. 16.	Cross section in the region of the line 16–16, Figure 15.
Fig. 17.	Diagrammatic cross section in the same region as Figure 16.
Fig. 18.	Cross section of the nipple-like anterior extremity.
Fig. 19.	The second section in a series of longitudinal sections. This is a portion of the bell, the outermost layer having been cut off with the first section from the middle of the figure, but remaining around the margin. In the centre is exposed the striated layer and the roots of the cilia arranged in quincunx.
Fig. 20.	Diagram of the condition shown in Figure 19.
Fig. 21.	Cross section in the region of the line 21–21, Figure 15, showing the radiating structure of the wall (*st. gran.*, Fig. 7) separating the anterior from the posterior half of the animal.
Fig. 22.	Longitudinal section showing an immensely thickened nuclear membrane.
Fig. 23.	Cross section in the region of the line 23–23, Figure 15.

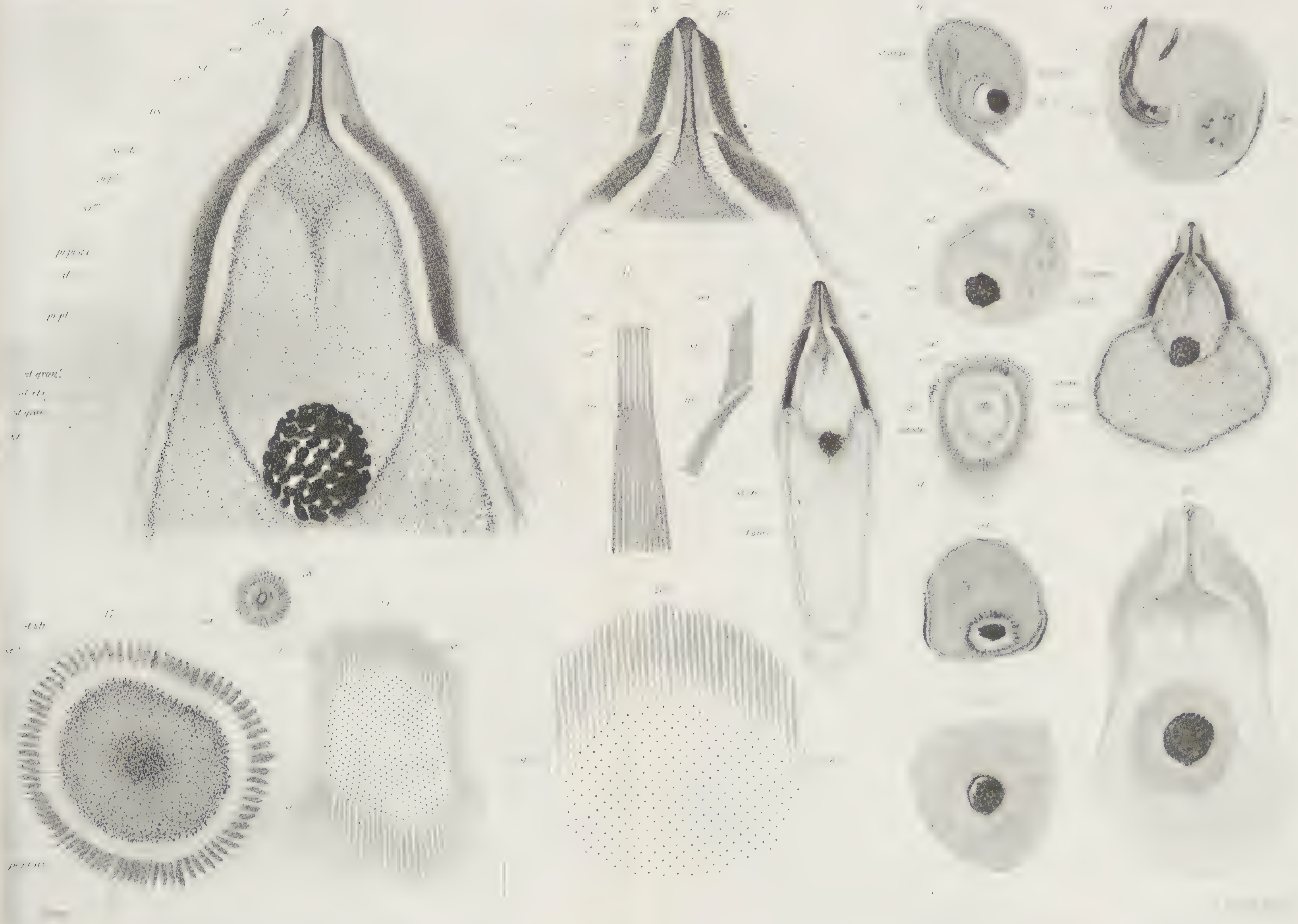

7
8
plc
ns
pp pl
st gran.
st gran
17

PLATE 3.

Figs. 24–26. Trichonymphæ showing conditions which may be preparatory to longitudinal division. Compare text. × 520.

Fig. 27. A parasite supposed by Leidy to be a young stage of Trichonympha. × 520.

Fig. 28. Another similar individual with a peculiar swollen cap. × 520.

Fig. 29. An individual more highly magnified. × 1100.

Figs. 30–32. Young heretofore considered as immature Trychonymphæ, but which I believe to be a distinct species. × 520.

Fig. 33. Longitudinal section of a Pyrsonympha. × 400.

Fig. 34. A Pyrsonympha containing wood fibre, the flagellum protruding in a tail-like appendage from the posterior or unattached end. × 400.

Figs. 35, 36. The same kind of parasite as is shown in Figures 30–32.

Fig. 37. The same kind of parasite as those shown in Figures 30–32, 35, 36, but drawn from a living specimen. × 520.

Fig. 38. The same as Figure 37, but just after death in normal salt solution. × 520.

Fig. 39. The same kind of parasite as that shown in Figure 37. × 520.

Fig. 40. A Pyrsonympha apparently in the act of engulfing a particle of wood fibre. × 400.

Fig. 41. A Pyrsonympha with a peculiar flagellum. × 520.

Figs. 42–44. The same kind of parasite as that shown in Figure 39. × 520.

[illegible] 3

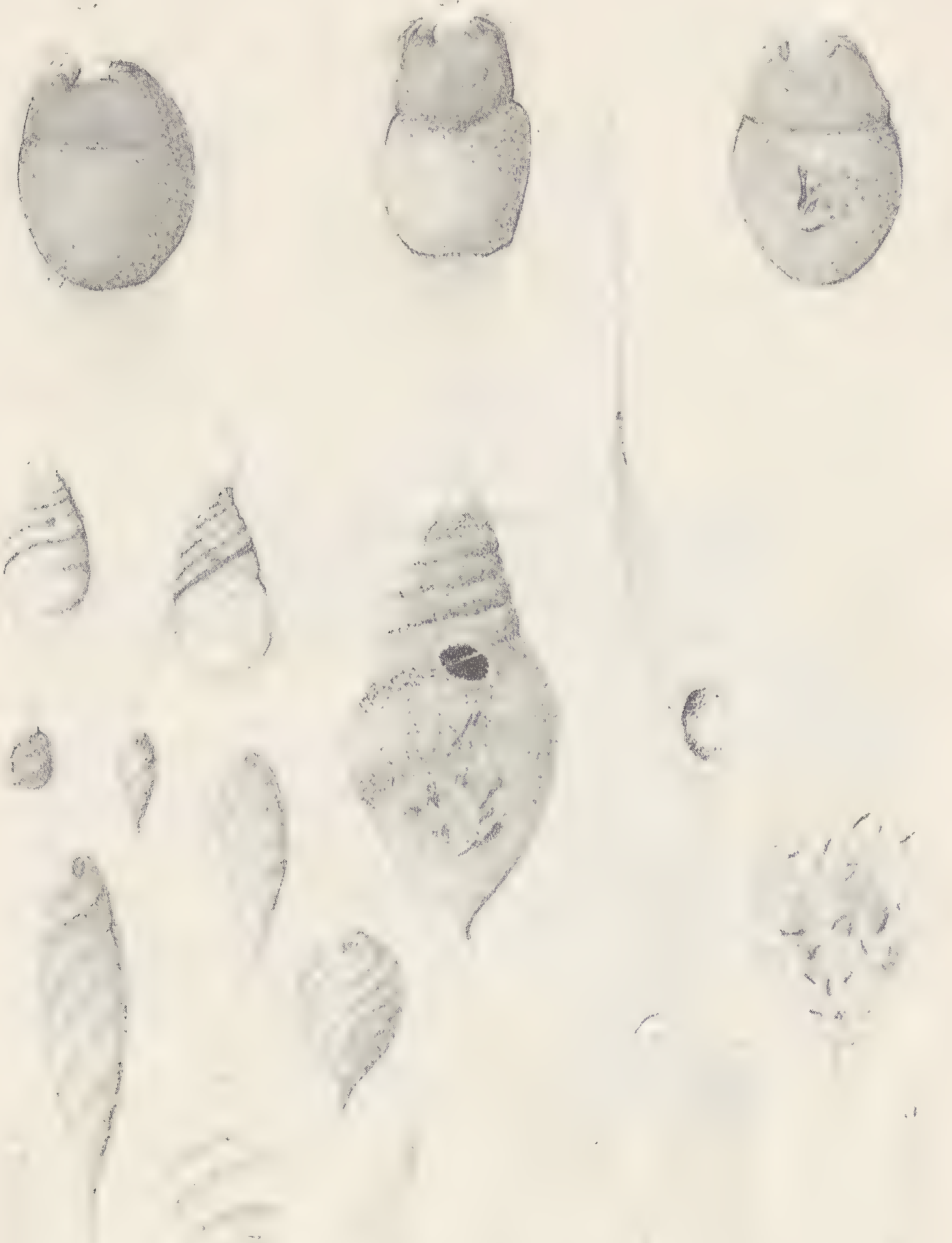


PLATE 4.

All figures are of Pyrsonympha vertens.

Fig. 45. Parasites attached by peduncles to a bit of the intestine of the host. Drawn from living specimens. × 400.

Fig. 46. Optical section of anterior portion of a Pyrsonympha, showing the relation of the knob-like structure (*tub.*) to the flagellum on one side and the peduncle on the other. × 1100.

Fig. 47. Anterior portion of an individual, showing the nucleus and the superficial muscular cords. × 1100.

Figs. 48, 49. Nuclei in stages of division.

Fig. 50. A very much attenuated nucleus.

Fig. 51. Surface view of a Pyrsonympha. Between the spiral muscular cords are bands of granular protoplasm. The region at *a* is bare of all muscular cords. At the extreme posterior portion are several ring-like markings (*ann.*). × 400.

Fig. 52. Cross section through the animal in the region of the nucleus. × 1100.

Fig. 53. Optical longitudinal section of a Pyrsonympha with its nucleus in the posterior half of the body. × 520.

Fig. 54. Portion of the surface of a Pyrsonympha, greatly magnified, showing a finer and a coarser set of muscular cords. The cords of the finer set are surrounded by a clear homogeneous substance, while granular protoplasm surrounds those of the other set.

Fig. 55. Optical section of the Pyrsonympha represented in Figure 51. There are two nuclei flattened against each other. × 400.

4

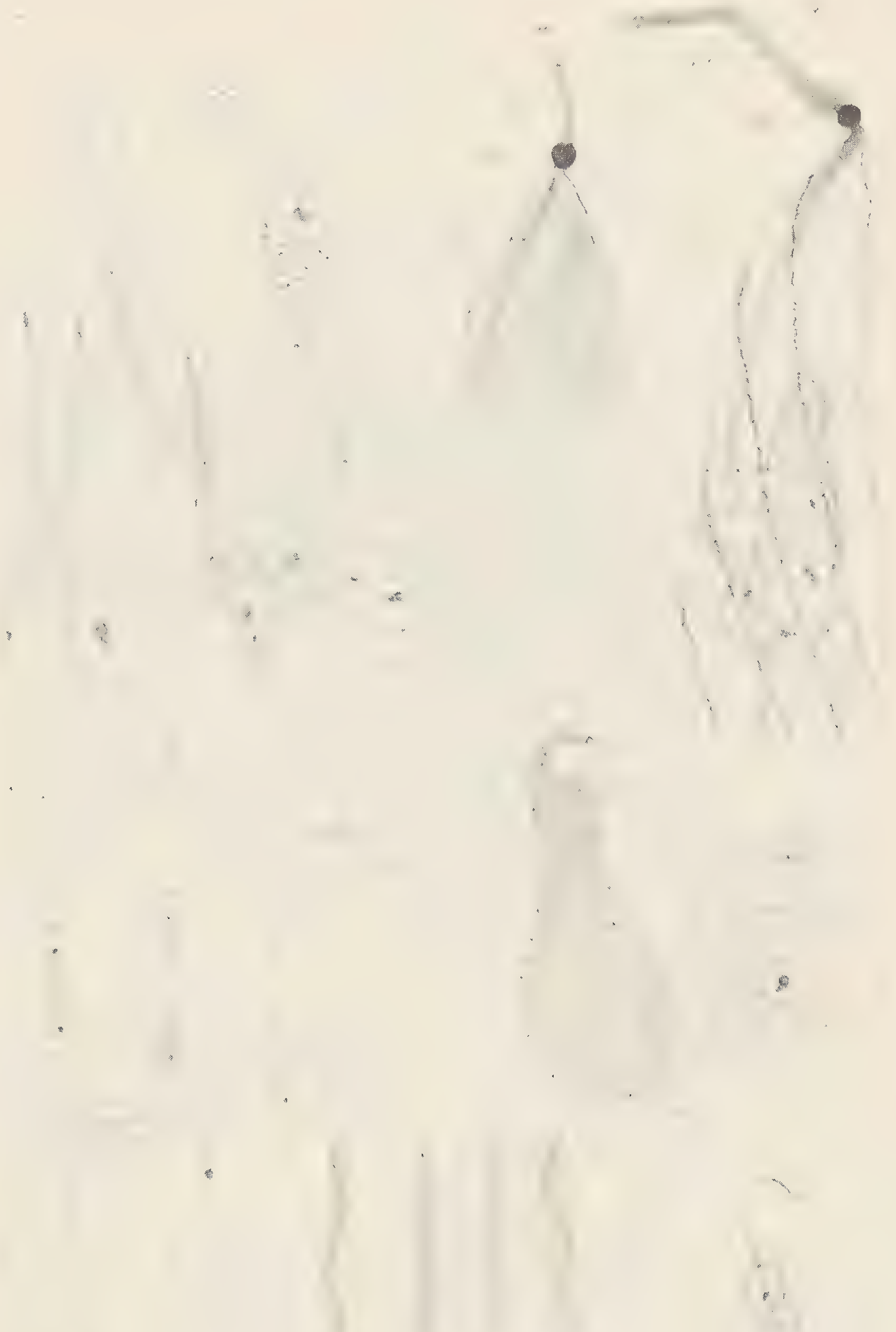


PLATE 5.

All figures are of Pyrsonympha vertens.

Fig. 56. Section of a portion of the intestine of a Termite, showing numerous young Pyrsonymphæ, the manner in which they attach themselves to the host, and the effect on the cells of the intestinal wall. × 1100.
a, a. Spaces due to shrinkage.

Fig. 57. Young Pyrsonympha without a flagellum. × 520.

Fig. 58. Young with a flagellum. × 520.

Figs. 59, 60, 65. Some of the shapes taken by a single living immature individual in the course of a few minutes.

Fig. 61. Young, showing that the flagellum takes the same direction as (is differentiated from ?) one of the superficial muscular cords. × 1100.

Fig. 62. Small Pyrsonympha, perhaps recently formed by division. × 520.

Fig. 63. Young Pyrsonympha without a flagellum. × 520.

Fig. 64. Small individual.

Fig. 65. Same individual as that shown in Figures 59 and 60.

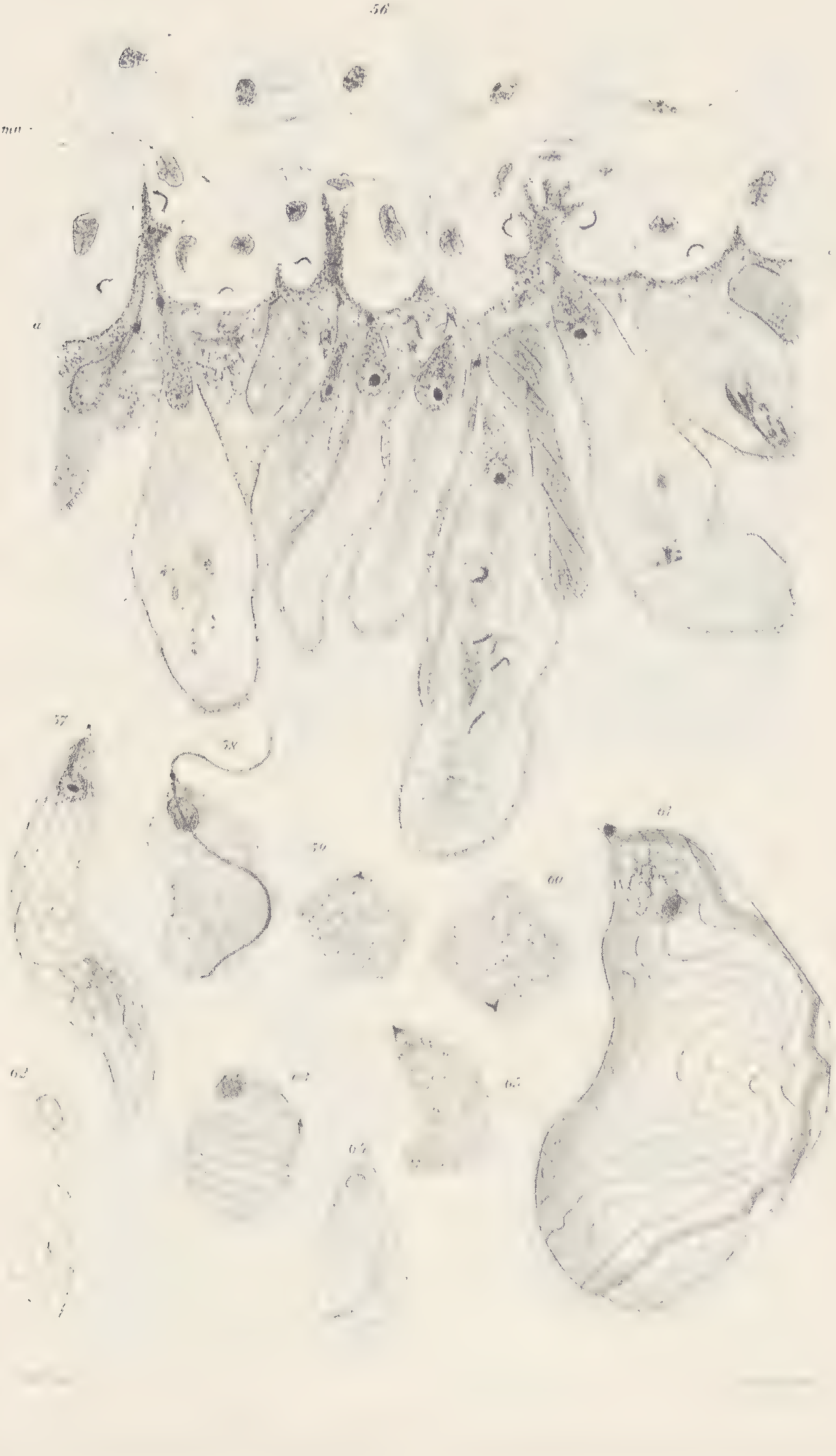

56
mn
a
57
58
59
60
61
62
63
64
65

PLATE 6.

Figs. 66–68. Common forms of Dinenympha. × 1100.

Figs. 69, 70. Surface views of the upper and lower sides of the same Dinenympha. × 1120.

Figs. 71, 72. Similar views of another individual. × 1120.

Figs. 73–76. Views of a Gregarine found as an intestinal parasite in Termes in company with Trichonymphidae.

Fig. 73. Normal appearance of a living Gregarine. × 520.

Fig. 74. A gregarine filled with sporocysts. × 430.

Fig. 75. Longitudinal section of a portion of the small intestine of a Termite, showing numerous Gregarines. × 150.

Fig. 76. Longitudinal section of a Gregarine. × 1100.

Bulletin of the Museum of Comparative Zoölogy
AT HARVARD COLLEGE.
Vol. XXXI. No. 4.

VARIATIONS IN THE BRACHIAL AND LUMBRO-SACRAL PLEXI OF NECTURUS MACULOSUS RAFINESQUE.

By F. C. Waite.

With Two Plates.

CAMBRIDGE, MASS., U. S. A.:
PRINTED FOR THE MUSEUM.
November, 1897.

No. 4. — *Variations in the Brachial and Lumbo-Sacral Plexi of Necturus maculosus Rafinesque.*[1] By F. C. Waite.

Variations in the position of the pelvic girdle in Vertebrates, especially in Amphibia, have already been noticed by several authors; Adolphi, Bourne, Case, Howes, G. H. Parker, and others. These variations, which obviously involve an inconstancy in the number of presacral vertebræ, are as a rule symmetrical, the entire girdle being one segment caudad — more rarely cephalad — to the usual position; but infrequent instances are found in which the right and left constituents of the girdle have unsymmetrical positions.

Closely associated with the pelvic girdle is the lumbo-sacral plexus, and the problem which suggests itself in this connection is to determine whether, with the variations known to occur in the skeletal structures of the girdle, there are correlated variations in the lumbo-sacral plexus.

If, as some morphologists believe, a difference in the position of the sacrum is the result of increase in the number of vertebræ by splitting of one or more presacral vertebræ, or decrease through fusion, then such phenomena must take place in one or the other, or both, of two regions, either anterior to the most posterior nerve of the brachial plexus, or between that point and the lumbo-sacral plexus.

To obtain evidence upon these alternatives, I dissected out the brachial plexus, in addition to the lumbo-sacral, in all the specimens which I have studied. As this plexus involves less variation than does the lumbo-sacral, I shall discuss it first.

In naming the spinal nerves, I have adopted the plan of calling that nerve which emerges between the cranium and first vertebra the first nerve,[2] succeeding nerves being consecutively numbered.

So far as I have noticed, there is little variation among either the sympathetic or dorsal branches of the spinal nerves. Since only the ventral branches enter the plexi, I shall, for the sake of brevity, designate the ventral branch of the first spinal nerve as nerve I, the ventral branch of the second as nerve II, etc.

---

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, E. L. Mark, Director, No. LXXXV.

[2] In the Anura, where there is no spinal nerve emerging anterior to the atlas, the so called first spinal nerve emerges between the first and second vertebræ, and is homologous to the second nerve of Urodela

It has seemed necessary in comparing plexi to indicate in some way the relative value of the nerves entering them. I have therefore recorded their approximate diameters, which I shall designate as their strength, — a rough method, but accurate enough for the present purpose.

The material which I studied consisted of thirty specimens of the large perennibranch salamander of the Middle United States, — Necturus maculosus Rafinesque. These specimens were obtained from the Great Lake Region, in the main from a single locality (near Sandusky, Ohio) on the south shore of Lake Erie.

Unfortunately, I neglected to note the sex of each individual. The importance of this did not occur to me until the urogenital system had been removed, and dissection had gone so far as to prevent the determination of the sex. The greater number (more than two thirds) were males, but which ones I am unable to say.

The work represented by this paper was done at the suggestion, and under the direction, of Dr. G. H. Parker, to whom I am indebted for assistance and advice during its progress.

THE BRACHIAL PLEXUS.

The brachial plexus (Plate **1**, Fig. 1) is formed from nerves I to V inclusive. In no case have I found indications that nerve VI contributed to it.

The greater strength of the plexus lies posterior to the pectoral girdle. Its major part is compacted into a large trunk, the brachial nerve (*br.*), which, after sending branches to the shoulder muscles, divides to supply the various muscles of the fore leg. But nerve distribution does not concern us here. It is my purpose to determine if, in the number and strength of the nerves which enter the brachial plexus, there be any variation which may be correlated with the variations in the sacral region.

If, when the sacral rib is on the 19th vertebra, — the more usual position, — we find the brachial plexus constant in position, and if, when the sacral rib is on the 20th vertebra, — a common variation, — we find a backward displacement of the brachial plexus to the extent of one segment, it would be fair to infer that the seat of variation is in the pre-brachial region.

Nerve I (Fig. 1) is slender, and does not contribute to the innervation of the appendage, but is distributed to the inner wall of the girdle. It often lies close to nerve II, and may (six cases in thirty) anastomose with it.

Nerve II is also slender, and is distributed to the same region as is I. It seems questionable if I and II can be properly considered parts of the plexus. In strength they approximate the ordinary post-brachial spinal nerves (VI to XV). In some cases branches of II run in close relation to the supracoracoid (*su'crac.*) branch of III, and may (four cases in thirty) pass out through the coracoid foramen with the supracoracoid. In no case have I found any anastomosis between branches of II and III, as implied by Hoffman ('74, p. 229) in his account of Necturus (Menobranchus); and from my specimens of Necturus I can assert that this is certainly not a constant relation, if indeed it occur at all.

Nerve III usually divides into three branches, of which the small anterior one is distributed to the thoracic wall, the middle one forms the supracoracoid nerve (*su'crac.*), while the larger posterior branch enters the main trunk of the plexus.

Nerve IV is usually the strongest trunk of the plexus. It passes directly to its exit posterior to the scapula, close to the margin of the glenoid cavity, giving off in its course a single small branch, which is distributed anteriorly on the thoracic wall. Before reaching the border of the scapula this nerve usually divides into two main branches, which pass side by side to the musculature of the anterior appendage.

Nerve V is the most posterior nerve to enter the plexus, its anterior branch joining nerve IV just before this reaches the scapula, while the small median and the posterior branches are distributed to the body wall, posterior to the girdle.

There were no variations of note in the *topography* of the plexi in the thirty animals examined, except in one case of slight want of symmetry in the point of junction of V with IV, but this occurred in a specimen which was normal in its sacral structures. Some variation occurs in the *relative strengths* of the nerves; for while IV is usually the strongest, it may be equalled by III, as was seen in six cases, of which four were with the sacrum in a normal position (19th vertebra), one with the sacrum on the 20th vertebra, and one with an unsymmetrical sacrum (Plate **2**, Fig. 5). Again, nerves III and V are usually of about equal strength, but III may be much (six to eight times) stronger than V, or more rarely may be weaker.

These conditions show a tendency toward variation in the location of the "strength-centre"[1] of the plexus, such variation usually resulting in displacement anteriorly; but this is not correlated with the variations in the position of the pelvic girdle, — indeed most such cases were found in specimens in which the pelvic girdle was normally placed, — nor have I found any correlation between the displacement of the strength-centre in the brachial and lumbo-sacral plexi respectively. This is not in accord with the conclusions of Adolphi ('96, p. 118), who says for Anura " . . . die beiden Extremitätenplexus, der Plexus sacralis und der Plexus brachialis, ihren Schwerpunkt in der gleichen Richtung verlegen . . ." Such a condition indicates that the variations in the brachial plexus are independent of variation in the position of the pelvic girdle; and since there is no posterior displacement of the brachial plexus, nor any change of topography in cases where the pelvic girdle is placed on the 20th vertebra, we have evidence that *there has been no interpolation of vertebræ in the part of the column anterior to the posterior limit of the brachial plexus.*

The Lumbo-Sacral Plexus.

The variations in the lumbo-sacral plexus are most conveniently grouped under three heads, viz.: A, those in which the girdle is attached to the 19th vertebra; B, those with the girdle carried by the 20th vertebra; and C, those in which the constituents of the girdle have an unsymmetrical position (see the Table, page 81).

Group A is represented by twenty specimens. The nerves here forming the plexus (Plate **1**, Figs. 2, 3) are XVIII to XXI inclusive, neither XVII nor XXII in any case entering it. The plexus is distributed by three trunks. The anterior is N. ileohypogastricus (*il-h'ga.*), which is the anterior branch of nerve XIX, and extends cephalad on the inner body-wall; its strength and relation to other nervous parts seem uniform. The middle trunk (*cru.*) is N. cruralis (obturator), which passes out between the ilium and pubis, to be distributed to the anterior part of the thigh. The posterior is N. ischiadicus (*isch.*), which is the main trunk, and is distributed to the posterior part of the thigh and to the leg.

We may distinguish in the topography of the plexus two types, based on differences in the source of the branches which go to form N. cruralis and N. ischiadicus; these I shall designate as α type and β type.

---

[1] The term "strength-centre" has been adopted to designate that point in the plexus which is central with regard to the combined "strengths" of the component nerves. We may thus conceive the whole "strength" of the plexus as concentrated at this point, the "strength-centre."

In the α type (Plate **1**, Fig. 2) N. cruralis (*cru.*) is formed from the union of the posterior branch of XIX with a small anterior branch of XX, while N. ischiadicus (*isch.*) is formed by union of the remaining part (posterior branch) of XX with the anterior branch of XXI.

In the β type (Plate **1**, Fig, 3) N. cruralis (*cru.*) is the middle branch of XIX, which may (three cases out of ten) receive a delicate branch from XVIII; while N. ischiadicus (*isch.*) is formed by union of the small posterior branch of XIX, all of XX, and the anterior branch of XXI.

It will be noticed that the α type (Fig. 2) presents, as compared with the β type, a tendency to a forward migration of the plexus as a whole, indicated by part of nerve XX trending forward into the next segment to enter N. cruralis; on the other hand, the β type (Fig. 3) shows a backward tendency, since nerve XIX sends a branch into the next posterior segment to enter N. ischiadicus, and also nerve XVIII occasionally enters into N. cruralis.

The successive spinal nerves in the region of the plexus may now be considered individually.

Nerve XVIII makes only a small and inconstant contribution to the plexus, since in three cases only, — all in the β type, — it gives a delicate branch to N. cruralis. Its strength is nearly constant, and is about the same as that of the ordinary spinal nerves anterior to it. This nerve may therefore be considered as a nearly typical spinal nerve.

Nerve XIX presents much variation in its strength relative to the other nerves of the plexus. It may equal XX, — six cases in twenty, — or it may have only $\frac{1}{4}$ the strength of that nerve. Its average strength as compared with nerve XX (the main nerve of the plexus) is between $\frac{1}{2}$ and $\frac{2}{3}$, and this is the relation usually found. Besides the ileo-hypogastric branch, which is constant, this nerve possesses one (type α, Fig. 2) or two (type β, Fig. 3) branches. In the β type the middle (cruralis) and posterior branches show considerable variation in strength in relation to each other.

Nerve XX is the chief nerve of the plexus. Its strength is usually about eight times that of an ordinary spinal nerve. In the α type, it gives off a branch anteriorly, which joins the posterior branch of nerve XIX, these together forming N. cruralis. This anterior branch is always much weaker than the remaining (posterior) one, which forms the major part of N. ischiadicus. In the β type the entire nerve becomes a part of N. ischiadicus.

Nerve XXI has a uniform relation to the plexus in the two types. Its stronger anterior branch enters N. ischiadicus, while the weaker posterior branch is distributed to the wall of the pelvic cavity. The strength of the whole nerve before branching varies from ¼ to ⅔ that of nerve XX, the average being between ⅓ and ½; i. e. it is usually weaker than nerve XIX, but may (four cases in twenty) equal that nerve in strength.

To gain evidence on the relation of the plexus to the skeleton, I have in each specimen determined the position of the first vertebra which bears a hæmal arch, for this is often assumed as a fixed point in discussing variations in the vertebral column. By reference to the Table on page 81, (see also Parker, '96, p. 712, and Bumpus, '97, p. 457,) it is seen that the position of the first hæmal arch is variable; but, as the following tabulations show, there is no correlation between these variations, and those of the "strength-centre" of the plexus as represented by the *α* and *β* types.

α type, with first hæmal arch on vertebra 22 = 4 cases.
α " " " " " 23 = 6 "
β " " " " " 22 = 6 "
β " " " " " 23 = 4 "

Group B includes the individuals having the sacrum borne on the 20th vertebra, and of these there were seven specimens. The nerves involved in the plexus (Plate **1**, Fig. 4) are XIX to XXII inclusive. Nerve XVIII in no case entered the plexus. In three cases a delicate branch from XIX was contributed to the formation of N. cruralis. Nerve XIX occupies the same relative position as did nerve XVIII in group A, but shows more of a tendency to enter the plexus (three cases in seven, as against three cases in twenty in group A) than did the element in the same position in group A. Moreover, it is distinctly (a half) stronger than are the ordinary spinal nerves. For these reasons it must be considered as belonging to the plexus.

Nerve XX corresponds in position and distribution to XIX in group A. In every case it branches into three parts, the anterior forming N. ileohypogastricus, the middle N. cruralis, and the posterior entering N. ischiadicus; i. e. the *β* type of group A only is represented, but with the modification that at first sight, the whole plexus is *apparently* one segment posterior to the position in the *β* type specimens of group A.

The whole of nerve XXI in each case enters into the formation of N. ischiadicus, for it sends no important branches cephalad or caudad. Its strength averages six times that of an ordinary spinal nerve, i. e. it is a fourth weaker than the nerve (XX) occupying the corresponding position in group A. Its average strength is about 1¼ times that of the next anterior nerve, while in group A the ratio is 1⅔ to 1.

Nerve XXII has here topographically the same relations as nerve XXI in group A, but its strength relative to the rest of the plexus is much less, and in two cases (in seven) *it fails to send a branch into the plexus.*

The position of the first hæmal arch is in every case on the 23d vertebra.

At first sight the whole plexus in group B seems to have moved with the girdle one segment caudad as contrasted with the position in group A, a condition which might be explained by the interpolation of a presacral segment; but for several reasons I do not believe such an explanation to be sufficient. If a presacral segment had been interpolated, thus entailing a change in position to the extent of an entire segment, we should expect still to see variations in the position of the first hæmal arch. In one half the cases in group A (see Table, p. 81) the first hæmal arch was on vertebra 23, *three* segments posterior to the main nerve of the plexus. Hence in group B, if the interpolation hypothesis be true, the hæmal arch ought to occur, at least occasionally, in the same relative position, i. e. on the 24th vertebra, instead of maintaining as it does a constant position on vertebra 23, only *two* segments posterior to the main nerve (XXI) of the plexus. The specimens examined by Parker ('96, p. 712) show the same result, i. e. a constancy of position of the first hæmal arch on the 23d vertebra in all specimens bearing the girdle on the 20th vertebra. Bumpus ('97, p. 473), however, among thirty-five specimens having this position of the girdle finds three (9%) in which the first hæmal arch is on vertebra 24. This shows that such a position, though possible, is rare.

Again, we should not expect the tendency of the last trunk nerve (XVIII in group A, XIX in group B) to enter the plexus to be so much greater in group B (43%) than in group A (15%), nor should we expect to find its strength in group B distinctly exceeding that of the ordinary spinal nerves, as it does, since there is no indication of such an excess in group A.

If interpolation has occurred, nerve XXII should show about the same average relative strength as the element (XXI) corresponding to it in group A. This is not found to be so, for XXII in group B is relatively and absolutely *much* weaker than XXI in group A, and by completely failing in two cases (28%) to enter the plexus shows an inconstancy not seen in the corresponding nerve (XXI) in group A. This leads to the conclusion that in group B this most posterior nerve (XXII) is not an essential element of the plexus.

Nerves XX and XXI in group B correspond, in position relative to the sacrum, to nerves XIX and XX in group A (cf. Fig. 4 with Figs. 2 and 3). In group A the main nerve (XX) has eight times the strength of an ordinary spinal nerve. In group B the main nerve (XXI) is but six times as strong as this unit. In group A nerve XIX has an average strength ½ to ⅔ that of nerve XX; though in some cases (30%) their strengths are equal, in others XIX may have only ¼ the strength of XX. In group B, on the other hand, in two cases only is XX weaker than XXI; in three cases their strength is equal, and in two cases XX is the *stronger*, i. e. in 70% of the cases XX equals or is stronger than XXI. The average strength of XX as compared with XXI is as 1.1 to 1 in group B, whereas in group A the ratio between the corresponding elements is about 0.6 to 1. This shows that in group B the main nerve (XXI) tends to be weaker, and the one next anterior to it (XX) to be stronger than the corresponding nerves (XX and XIX) in group A. This, together with the weakness and inconstancy of XXII in group B, and the greater strength of XIX with its increased tendency in this group to enter the plexus, is evidence that in group B the *strength-centre of the plexus has not travelled caudad through an entire segment* as compared with group A, *but holds a position intermediate* between such an one and that of group A.

If we adopt as an explanation of the above facts and conclusion the interpolation of a presacral segment, we shall have to supplement such an explanation by assuming a subsequent movement cephalad of the plexus as a whole, to account for the ascertained intermediate position of the strength-centre of the plexus.

From the evidence of the hæmal arch, and of the topography (β type) of the plexus, — which I shall immediately discuss, — it seems more reasonable to consider this intermediate position of the plexus the result of what may be called the migration caudad of the locus of the strength-centre. The correlation of the position of this locus with that of the girdle I shall discuss further on.

There is in group B a persistence of the β type of topography. This at first may seem to contradict the conclusion that we have an intermediate position of the locus of the strength-centre, for with an intermediate position of the plexus arising from migration caudad we should expect traces of reversion toward the more anterior position, such as is indicated by the tendency cephalad in the α type. However, there are reasons for expecting the β type here. (1) In such posterior migration as is shown in group B, there must also be a tendency — whatever has been the stimulus to cause the migration of the locus of the whole plexus — for a movement caudad among the parts of the plexus, since the movement of the entire plexus is but the summation of the movements of its elements, the individual nerves. (2) Nerve XXII is so inconstant and contributes so feebly to N. ischiadicus, that, in compensation for this deficiency, all of XXI is taken up to form N. ischiadicus, and thus it can contribute nothing to N. cruralis. Again, I have shown that, in group B, XXI is relatively weaker, and XX relatively stronger than the corresponding elements of the plexus in group A. Hence a contribution from XX to N. ischiadicus (in group B) serves to make up the deficiency arising from the inconstancy and stronger posterior tendency of XXII (cf. Fig. 4). (3) It is to be noticed that in group A (Figs. 2 and 3), XXI *always* entered N. ischiadicus and that nerve *only*, while XX was (see Table) in many cases (α type) divided between N. ischiadicus and N. cruralis. This gives to XX the definite relation of a component part to N. cruralis in group A, a relation which might be expected to be retained after migration, i. e. in group B. But in group A XXI in no case had any relation to N. cruralis. It is therefore less probable that in the new condition XXI should form a new connection entering N. cruralis, than that it should give its entire strength to N. ischiadicus, as it does, with which it had the definite relation of a component part in the old condition. The general backward movement of the parts of the plexus, and the former (α type of group A) branched condition of XX, may account for the fact that this nerve sends a branch to N. ischiadicus in this post-migration condition.

These considerations lead me to believe that the β type is the only condition to be expected in group B, if the plexus has reached its position there by means of migration of the locus of its strength-centre. If however, interpolation of a presacral segment has occurred, we should expect to find about the same variations in type of topography in group B as in group A. These do not occur, therefore the persistence of the β type of topography in group B; the inconstancy of nerve XXII, and the added activity of XIX in their contributions to the plexus; together with the slight variation in the position of the first hæmal arch shown in this group; — all combine as evidence against the theory that the position of the pelvic girdle in group B is the result of interpolation of a presacral segment.

Group C includes three individuals (10% of the total number examined), in which the attachment of the girdle is unsymmetrical.

Of these one (Plate **2**, Fig. 5) bore the right sacral rib on the 19th vertebra, the left on the 20th, while the first hæmal arch was on the

23d vertebra. The topography of the plexus is of the α type. There is no asymmetry in its distribution to the appendages, although the plexus of the left side must as a whole trend further caudad in order to reach the foramina of exit. On the left side the backward trend of XIX exposes a longer antero-posterior area of the body wall to which XVIII is distributed than is exposed on the right side. In accordance with this, nerve XVIII of the left side is slightly stronger than its companion of the right side. Also nerves XIX and XX of the right side are somewhat stronger than their mates of the left side; i. e. the strength-centres of the two sides are to a slight extent unsymmetrically placed, but this by no means equals the extent of an entire segment.

To which group, A or B, is this specimen more closely related? As in both these groups the first hæmal arch may occur (see Table) on the same vertebra as in the specimen under consideration, this criterion is of no value in determining the affinity of the specimen. But the fact that the plexus of this specimen is of the α type indicates that it falls under group A, to which this type is restricted (see Table). A glance at Figure 5 shows that the main nerve of the plexus is XX, and that XXII fails to enter the plexus, both conditions typical of group A. Hence I consider this specimen to represent an individual like those of group A, in which, however, the sacral rib of the left side is displaced one segment caudad. There is not a corresponding displacement through one segment of the plexus of the left side, but only a *slight* displacement of the strength-centre caudad.

The two other unsymmetrical specimens (Plate **2**, Fig. 6) have in each case the right sacral rib on the 18th vertebra, the left upon the 19th. In both cases the first hæmal arch is on the 22d vertebra. The plexus is of the β type, but with the modifications that in both cases the posterior branch of nerve XVIII enters strongly into the plexus, and further in both cases nerve XXI does not enter the plexus, but remains a weak nerve distributed to the wall of the pelvic cavity. The plexus is consequently formed of nerves XVIII, XIX, and XX. Nerve XVIII is stronger than usual, XIX equals the strength of XX, and, as noted, XXI is very weak, being no stronger than an ordinary spinal nerve, all of which shows a displacement of the strength-centre cephalad. I can detect no marked want of symmetry in the locus of the strength-centre of the two sides, but if there be any, indications are that it is toward a yet further displacement cephalad of the plexus of the right side.

The position of the hæmal arch on vertebra 22 and that of the sacral ribs remove these two specimens from any relationship to group B, and I therefore conclude that they represent individuals like those of group A, in which the right sacral rib has been displaced cephalad through one complete segment. Superimposed upon this is a displacement cephalad of the strength-centre of the plexus through the extent of part of a segment only, as is clearly indicated by failure of XXI to enter the plexus, and the increased strength of XVIII. These conditions together represent a state intermediate between that of individuals bearing the girdle symmetrically on the 19th vertebra, and a hypothetical group in which the girdle would be carried symmetrically on the 18th vertebra, and probably with the first hæmal arch on the 21st vertebra part of the time at least. Such a variation has not been described in Necturus, so far as I know, but I think it likely to occur, although the prevailing tendency in abnormal position of the girdle is toward displacement caudad. Indeed, Davidoff ('84, p. 412) has found such symmetrical displacement cephalad in Salamandra maculosa.

Of the 157 specimens of Necturus recorded by Parker ('96), Bumpus ('97), and myself, thirteen (8 %) are found to have unsymmetrical sacra. Of these thirteen, nine have the sacral rib of the left side further cephalad, four that of the right side. It is thus seen that unsymmetrical sacra are not very rare, and further that either side may be in advance. Of these four specimens with the right side in advance, three, one recorded by Bumpus ('97, p. 466) and two by myself, invade the territory of the 18th segment, and these three are the only cases out of the 157 in which that segment is invaded.

By way of summing up the statistics of certain of the conditions described, the following table of the thirty specimens which I have dissected is inserted: —

TABLE.

Vertebra which carries Sacrum.	Number of Specimens.	α Type.	β Type.	First Hæmal Arch on	
				Vertebra 22.	Vertebra 23.
19	20	10	10	10	10
20	7	0	7	0	7
19 (rt.) and 20 (lft.)	1	1	0	0	1
18 (rt.) and 19 (lft.)	2	0	2	2	0

An interesting skeletal variation in one of the specimens of group C just described is the occurrence on the left side of the 19th vertebra of a bifurcate transverse process and a partially double sacral rib (Plate **2**, Fig. 7). The two sacral ribs are not distinct throughout their course, but articulate independently with the transverse processes, and normally with the ilium. This condition is parallel with the occurrence of bifurcated transverse processes on the vertebræ of Rana, as recorded by Bourne ('84, p. 87).

There has lately come into my possession a skeleton of this species, the soft parts of which had already been to a considerable extent removed. This skeleton shows (Plate **2**, Fig. 8) a single sacral rib on the left side borne on the 19th vertebra, while on the right side are *two* sacral ribs borne one each on the 19th and 20th vertebræ. These ribs are both well formed, but the posterior one is much the shorter, and from comparison with the other side, is evidently the supernumerary rib. Each articulates independently with the head of the ilium, and all the joints work easily. The transverse process on the left side of the 20th vertebra shows no trace of a rib or articulation, and as it was well covered with the musculature, which had not been disturbed when I received it, I am certain that none existed there. The condition of the specimen when received was such as not to allow determination of the nerve relations.

Theoretic Considerations.

The variations which have been described in the preceding pages involve at least two questions : (1) Does the abnormal position of the girdle arise by intercalation or excalation of presacral segments, by slipping of the girdle upon the column cephalad or caudad, or by some other means ? (2) Is there any correlation between the variations of the plexus and those of the girdle, and if so, of what sort is it ?

The first of these questions is far reaching, and this paper does not aim at an exhaustive discussion of it. It is commonly held that nerves are less subject to variation than either muscles or skeletal parts, and thus serve as a surer basis for homology ; yet this basis is in a degree unstable, for there are certainly considerable variations amongst nerves, as I have shown, for instance, in the lumbo-sacral plexus.

The evidence for intercalation or excalation as an explanation of the changes in the presacral length of the column is of a diversified nature, and the opinions concerning such a process may be roughly grouped in two categories : first, that the change in number of segments is due to an initial variation in the serial number and position of centres of metamerism, — a doctrine formulated by Bateson ('92, p. 111); and, secondly, that such change arises from fusion of two or more adjacent somites, or from the splitting of one or more somites somewhere in the presacral region. The first of these two views is the more acceptable as a morphological process, as it preserves the integrity of the metameres and makes the process a general one affecting the animal as a whole, rather than localizing the activity within narrow limits, but the evidence in its favor is mostly *a priori*.

Rosenberg ('76, p. 104) was one of the first to advance such a view, but he went further than is implied in the above statement, and held that this process is an actively phylogenetic one, and that in the vertebrate series its operation results in a constant shortening of the vertebral column. This shortening is greatly emphasized in some orders, e. g. Anura, whereas such conditions as occur in Ophidia must, on the contrary, be considered reversionary.

According to his view, in the early ontogeny there is represented the primitive condition with a very large number of separate prosegments, but in course of development of the individual these are reduced to the number set by heredity. We may infer variation in the final number of segments to be the result of inaccuracy of response to the hereditary stimulus. As noticed by many writers upon this subject, the great majority of such variations are toward an increase in the number of segments, and according to this view such cases must be interpreted as atavistic. It would seem that Rosenberg's view is insufficient, or at least if there be such a general tendency, it is exerted, not in a single unilateral series, but in a branching series of phylogenetic relationships.

In such cases of variation between two individuals either of the same or of different species, no one centre of the final series of metameres in the normal can be directly homologous with any one centre in the variant; i. e. the number of segments arising in the variant differs from that arising in the normal, and each segment occupies a new position different from that in the normal.

Most of the evidence from recorded skeletal abnormalities better fits the second category stated. Baur ('91, p. 335) claims intercalation of vertebræ as an actual ontogenetic process. This is based upon the evidence afforded by certain complexes of vertebræ which show incomplete fission on one side of the median plane, with a normal condition on the other side, these having been recorded in some Ophidia by Albrecht, Owen, and Baur himself. Other cases of vertebral "masses" have been described by Bourne ('84, p. 86), Benham ('94, p. 477), Adolphi ('96, p. 133), and others. But such masses may, in my opinion, better be interpreted as ankylosis, symmetrical if the line of fusion be transverse to the axis of the column, or unsymmetrical if the line of fusion has been oblique. This is borne out by the fact that near, though not necessarily contiguous to such an unsymmetrical mass, there is usually found a complementary mass (see Benham, '94, pp. 477, 478) ; i. e. if by oblique fusion we have a mass containing one right half-vertebra and two left halves, we shall find near by another mass representing one left half-vertebra, and two right halves. The vertebræ lying between these two masses will be morphologically oblique, their two halves in each case belonging to different somites, although the adjustment of growth may have brought these to an apparently normal position, with transverse axis at right angles to the main axis of the column. That the right and left halves of a vertebra may slide upon each other, is held by Adolphi ('96, p. 136) to be confirmed by embryological evidence. Such unsymmetrical masses have not been accompanied by correlative asymmetry in musculature and nerves where the soft parts have been described.

Symmetrical fusion of vertebræ has been described by Howes ('93, p. 295), Adolphi ('95, p. 466, and '96, p. 122), and others. An actual increase in number of vertebræ, and also an indicated increase by grooving and partial splitting of vertebræ, and by bifurcation of transverse processes, have been noticed by Bourne ('84, p. 87), Benham ('94, p. 478), and others. The cases of actual increase described were in Anura, and resulted from separation of the anterior portion of the urostyle as a supernumerary vertebra. Adolphi ('95 and '96) has recorded forty-three cases of vertebral fusion in Bufo, Pelobates, and Rana, and has determined the nerve relations. He finds that in such cases of fusion the spinal nerves are not suppressed, but emerge through foramina in the fused mass; they are, however, liable to be weaker than normal.

Such supposed direct evidence of intercalation and excalation is capable of being interpreted as pathological, rather than as a disturbance tending primarily to alter the serial number of metameres, — especially since it is almost entirely confined to the skeleton, without involving musculature or nerves beyond the narrow limits necessitated by local accommodation to the distorted vertebræ. No evidence of the inheritance of such abnormalities has yet been offered. Such would be valuable as determining whether or not these variations show persistence. If so, it would indicate that they are sports; if not, the pathological interpretation would be strengthened.

I have shown that no intercalation or excalation is evident in the prebrachial region of Necturus, and since serial variation tends to be at one end of the series, it is more to be expected in the prebrachial region than in the postbrachial-presacral region. Addition or loss at the caudal end of the series may be disregarded, as this could not directly affect the number of presacral vertebræ, although it might be correlated with an abnormal position of the sacrum, both being an indication of general instability in the individual.

While the idea of variation in the number and position of centres of metamerism may be attractive on theoretic grounds, it has no observational evidence to support it, and, further, is insufficient to account for unsymmetrical sacra and supernumerary sacral ribs. On the other hand, intercalation or excalation has not been shown to exist as a morphological process, the supposed evidence for it being more naturally interpreted as due to pathological conditions. Since these two explanations seem improbable, we must look for some other cause of the variations of presacral distance which we find.

The common expression of sliding or shoving of the sacrum upon the column is open to criticism. It is contrary to ideas of metameric unity that the girdle should begin its development in one segment, and later in ontogeny migrate to the next. Bolk ('94, p. 267) has found in Homo during ontogeny an actual migration cephalad on the part of the Anlage of the pelvic girdle; but such migration is confined within narrow limits, not having extended over an entire segment, and thus the Anlage has not passed through a myotome. A slight migration of the musculature in relation to the skeleton is also known, but none of these slight changes are sufficient to account for sudden displacement of the girdle through an entire segment. Bumpus ('97, p. 464) has advanced a modification of this idea to account for the greater frequency of displacement caudad. Since the transverse processes to which the sacral ribs are attached lie nearer the caudad limit of the vertebra, he considers it "more probable that variations occurring in the course of ontogenetic development will fall on the side of nearer proximity," i. e. into the next segment caudad, and, having once invaded the territory of this new segment, the ribs will be adjusted to the proper position within that segment near the posterior limit. The individuality of segments in the skeleton is very sharp, and any explanation which involves a migration of an organ located entirely in one segment, so that it comes to lie wholly in another segment, assumes a process which is not only unproved, but seems to me highly improbable. Bumpus accounts for variation of the serial position of the sacrum by assuming that the appendage has a locus fixed at a point whose linear distance from the cranium is a definite and constant proportion of the entire length of the animal. The change in serial position of the girdle is then effected by compressing the presacral vertebræ, making each shorter and diminishing their combined length, thus bringing a vertebra caudad to the normal, opposite the stationary appendage locus. While such a view may be made to account also for asymmetrically placed sacra, it is difficult to see how it will adapt itself to the occurrence of supernumerary sacral ribs, and especially those asymmetrically placed (see Plate **2**, Fig. 8).

What seems most probable is that in different individuals the girdle may develop at primarily different distances (measured in segments) from the cranium. In Necturus we find a pair of sacral ribs on vertebra 19 (group A), or on 20 (group B). The explanation by intercalation implies that vertebra 20 in group B is the same vertebra as 19 in group A. That of slipping of the girdle — literally taken — implies that a girdle beginning to form in the 19th segment later (in ontogeny) is transferred to the 20th segment. Both explanations, as already stated, seem unsatisfactory. It is more logical to consider that the new position of the girdle is due to a stimulus to girdle formation having been applied at a *new* point, i. e. in a segment other than the normal, and hence that a sacral rib may arise in any one (or more, as shown in supernumerary ribs) of several points in this region. In Necturus these points are at least three, located in the 18th, 19th, and 20th segments.

Such a view explains the variation as to place of origin in different segments of sacra placed symmetrically, and also the condition of unsymmetrical sacra, such as have been described in group C, — since the stimulus to girdle formation is not single but paired, i. e. from the future appendages, and so need not necessarily be symmetrical; and above all it is sufficient to explain the occurrence of supernumerary sacral ribs. These latter may be on one side only (Plate **2**, Fig. 8, Howes, '86, p. 279, Lucas, '86, p. 562, and others); or a symmetrical pair of supernumerary ribs may appear (Case, '96, p. 232; Lucas, '86, p. 562).

From the foregoing discussion I conclude that *neither intercalation or excalation, nor slipping, are involved,* but that the abnormal position of the girdle represents development of a *new* girdle at a *new* point.

This new position is usually caudad to the normal, though in a few recorded cases in Urodela (Davidoff, '84, p. 412, and others) it is cephalad. Such general displacement caudad is capable of interpretation either as atavistic, or as indicating some force at work tending to lengthen the vertebral series.

It is noticeable that unsymmetrical relations of the appendages are more frequently recorded in Amphibia than in Reptilia, Aves, or Mammalia. This may possibly be due simply to the probably greater number of Amphibia examined. But assuming that this is not the case, it is not clear why such variation should exceed in this class. I offer, however, the suggestion that it may be due to the position of the embryo during development. In Amphibia the position is such that the embryo is curled within the egg membrane *laterally*, which would tend to shorten the concave side, and so might induce a displacement of the appendage of that side cephalad or caudad. In the other groups mentioned, the curling of the embryo is *dorso-ventrally*, and would give less tendency to unsymmetrical relations.

As to the second question involved, — Is there any correlation between the variations of the plexus and those of the girdle? — there is a wide difference of opinion, ranging from very close correlation, as maintained by Ruge ('93, p. 393), to no correlation, as believed by von Ihering ('78), who regards nerve and skeleton as independent in variation. Von Ihering holds that the plexus migrates as a whole independently of the girdle; if cephalad, then a presacral pair of spinal nerves drops out, if caudad, a pair is inserted, and if the migration be unsymmetrical, it involves loss or addition of a spinal nerve on one side only.

Such a scheme, by reason of its apparent artificiality, fails to appeal to me strongly, and no conditions found in Necturus warrant adoption of such a hypothesis.

The plexus is a combination of spinal nerves, the nature of whose topography is secondary. The point which needs emphasis in this connection is that the variation of the plexus is not a variation as a whole, but the summation of variations of its elements (individual spinal nerves). The variation in strength of these elements is probably a response to the influence from their end organs, — the muscles, — for there appears to be direct correlation between the size and activity of a muscle, and the strength of the nerve or nerves supplying it. Whether the muscles of a given metamere shall develop as limb muscles, i. e. muscles of increased size and activity, or into less extensive trunk musculature, depends upon whether or not in that region an appendage — the primary determinant of both plexus and girdle — is to arise. If appendicular musculature develop, the increased activity presumably induces stronger development of nerves in the segments involved, the matter of topography of plexus being secondary to the determination of the segmental position of the appendage.

That there is any direct correlation between skeletal and nervous tissues seems improbable, for there is no obvious reason why nerves should directly influence skeletal parts, nor is it probable that skeletal parts directly influence the position of nerves, since the vertebrate skeleton arises, both in phylogeny and in ontogeny, much later than the nervous system.

The view of the relations of nerve and skeletal parts, first hinted at by Fürbringer ('79), and more clearly formulated by Eisler ('92), seems much more reasonable than the idea of direct correlation. According to Eisler's conception, skeletal and nervous structures exhibit variations independently, but in parallel directions. The control of such parallelism rests with the musculature. The latter has very definite relations to the nerves on the one hand, and to the skeleton on the other. Bolk ('94) has shown that in Homo the position of the nerves depends upon the position of the muscle segment, which is differentiated earlier than the nerve, and it is also well known that the myomeres have very close relations to the vertebræ, so that in any given segment there is an interdependence among the three systems. Either nerve or vertebra may vary within certain limits, without necessarily affecting the other, but extensive variation of either would presumably influence the other through intermediation of the musculature.

From the nature of the case skeletal variations within narrow limits are less easily observable than nervous; but the examination of almost any series of vertebræ shows variation not only serially, but also on the right and left sides of the same vertebra. Such variations have been recorded by Paterson ('92, pp. 523, 524) from dissections of a large series (265) of human adults.

The conception of parallel variations of skeleton and nerve under control of the musculature is able to explain the fluctuations in position and strength of nerves belonging to any one segment involved in the plexus. It also offers an explanation of the inverse correlation of nerves of adjacent segments, seen in the weakening of the nerve of one segment, accompanied by a strengthening of that of the next segment; for since many muscles are innervated by two or more nerves from different segments, if one of these becomes weaker, the other becomes stronger to make up the deficiency. It should be remembered further that it has been shown that any one of several myotomes in this region is able to produce sacral ribs. In the greater number of cases the function of rib production by the myotome is expressed at a constant distance (measured in metameres) from the cranium, resulting in what we call the normal position; but as some tendency arises for the girdle to be abnormally placed, such tendency is expressed by the appearance of a *new plexus* and a *new girdle* in a *new* position. However, as we have seen in group B, the plexus in the new position does not have the same relation to the girdle-bearing segment that it did in the old; on the contrary, it tends to occupy a place intermediate between such a position and the old one. The girdle also may possibly show a parallel intermediate position; but if so, it is more difficult to verify. Such an intermediate position of the plexus may be interpreted either as representing an atavistic tendency, or an incomplete migration. I am inclined to believe in the latter, and that it indicates a less complete response by the plexus than by the girdle to the influence of the musculature which changes the locus of both girdle and plexus.

The nerve relations in Necturus show that variations of girdle and plexus are nearly parallel, but that these are in some degree independent, as exhibited by the fact that the strength-centre of the plexus does not have just the same relation to the girdle in the variant that it had in the normal condition.

February 20, 1897.

NOTE. — Since the manuscript of this paper left my hands, two papers bearing upon the question of intercalation have appeared.

Ridewood ('97, p. 366) considers that the point of sacral rib formation and attachment is determined by some stimulus external to the column, and that the girdle does not migrate from one segment to another during ontogeny, — a conclusion which is along the same line as my own (pp. 85, 87).

Baur ('97) contends for intercalation as an ontogenetic process, but I find little in addition to what is contained in his earlier paper (Baur, '91), except that he now (p. 42) supports the idea that the pelvis, developing in one segment, may migrate into a neighboring segment, and become "secondarily united with the vertebral column."

October 1, 1897.

BIBLIOGRAPHY.

Adolphi, H.
'93. Ueber Variationen der Spinalnerven und der Wirbelsäule anurer Amphibien. I. Morph. Jahrb., Bd. XIX. p. 313.

Adolphi, H.
'95. Ueber Variationen u. s. w. II. Morph. Jahrb., Bd. XXII. p. 449.

Adolphi, H.
'96. Ueber Variationen u. s. w. III. Morph. Jahrb., Bd. XXV. p. 115.

Bateson, W.
'92. On Numerical Variation in Teeth, with a Discussion of the Conception of Homology. Proc. Zoöl. Soc. London, 1892, p. 102.

Baur, G.
'91. On Intercalation of Vertebræ. Jour. Morph., Vol. IV. p. 331.

Baur, G.
'97. Remarks on the Question of Intercalation of Vertebræ. Zoöl. Bull., Vol. I. p. 41.

Benham, W.
'94. Notes on a particularly Abnormal Vertebral Column of the Bull-frog (Rana mugiens); and on certain other Variations in the Anuran Column. Proc. Zoöl. Soc. London, 1894, p. 477.

Bolk, L.
'94. Beziehungen zwischen Skelet, Muskulatur, und Nerven der Extremitäten. Morph. Jahrb., Bd. XXI. p. 241.

Bourne, A. G.
'84. Certain Abnormalities in the Common Frog (Rana temporaria). Quart. Jour. Micr. Sci., Vol. XXIV. p. 83.

Bumpus, H. C.
'97. A Contribution to the Study of Variation. (Skeletal Variations of Necturus maculatus Raf.). Jour. Morph., Vol. XII. p. 455.

Case, E. C.
'96. Abnormal Sacrum in an Alligator. Amer. Naturalist, Vol. XXX. p. 232.

Davidoff, M. von.
'84. Ueber die Varietäten des Plexus lumbosacralis von Salamandra maculosa. Morph. Jahrb., Bd. IX. p. 401.

Eisler, P.

'92. Der Plexus lumbosacralis des Menschen. Abhandl. Naturf. Gesell. Halle, Bd. XVII. p. 279.

Fürbringer, M.

'79. Zur Lehre von den Umbildungen der Nervenplexus. Morph. Jahrb., Bd. V. p. 324.

Hoffmann, C. K.

'74. Klassen und Ordnungen der Amphibia. *In* Bronn's Klassen und Ordnungen des Thier-Reiches. Bd. VI. Abth. II. Lief. 6 u. 7. Leipzig u. Heidelberg.

Howes, G. B.

'86. On some Abnormalities of the Frog's Vertebral Column. R. temporaria. Anat. Anz., Jahrg. I. p. 277.

Howes, G. B.

'93. Notes on Variation and Development of the Vertebral and Limb Skeleton of the Amphibia. Proc. Zoöl. Soc. London, 1893, p. 268.

Ihering, H. von.

'78. Das peripherische Nervensystem der Wirbelthiere als Grundlage für die Kenntniss der Regionbildung der Wirbelsäule. Leipzig, 1878.

Lucas, F. A.

'86. The Sacrum of Menopoma. Amer. Naturalist, Vol. XX. p. 561.

Parker, G. H.

'96. Variations in the Vertebral Column of Necturus. Anat. Anz., Bd. XI. p. 711.

Paterson, A. M.

'92. The Human Sacrum. *Abstr. in* Proc. Roy. Soc. London, Vol. LI. p. 520.

Ridewood, W. G.

'97. On the Development of the Vertebral Column in Pipa and Xenopus. Anat. Anz., Bd. XIII. p. 359.

Rosenberg, E.

'76. Ueber die Entwicklung der Wirbelsäule und das Centrale Carpi des Menschen. Morph. Jahrb., Bd. I. p. 83.

Ruge, G.

'93. Verschiebungen in den Endgebieten der Nerven des Plexus lumbalis der Primaten. Morph. Jahrb., Bd. XX. p. 305.

DESCRIPTION OF PLATES.

The Arabic numerals indicate the serial number of the vertebræ, the Roman numerals the serial number of the ventral branch of the spinal nerves.

ABBREVIATIONS.

br.	Nervus brachialis.	*il-h'ga.*	Nervus ileohypogastricus.
cru.	Nervus cruralis	*isch.*	Nervus ischiadicus.
cst. scr.	Sacral rib.	*prc. t.*	Transverse process.
cst. scr'.	Supernumerary sacral rib.	*su'crac.*	Nervus supracoracoideus.
il.	Ilium.		

All the diagrams are drawn to natural scale of a full grown individual, and are viewed from ventral aspect. The size of nerves is drawn to scale roughly for the average condition.

PLATE 1.

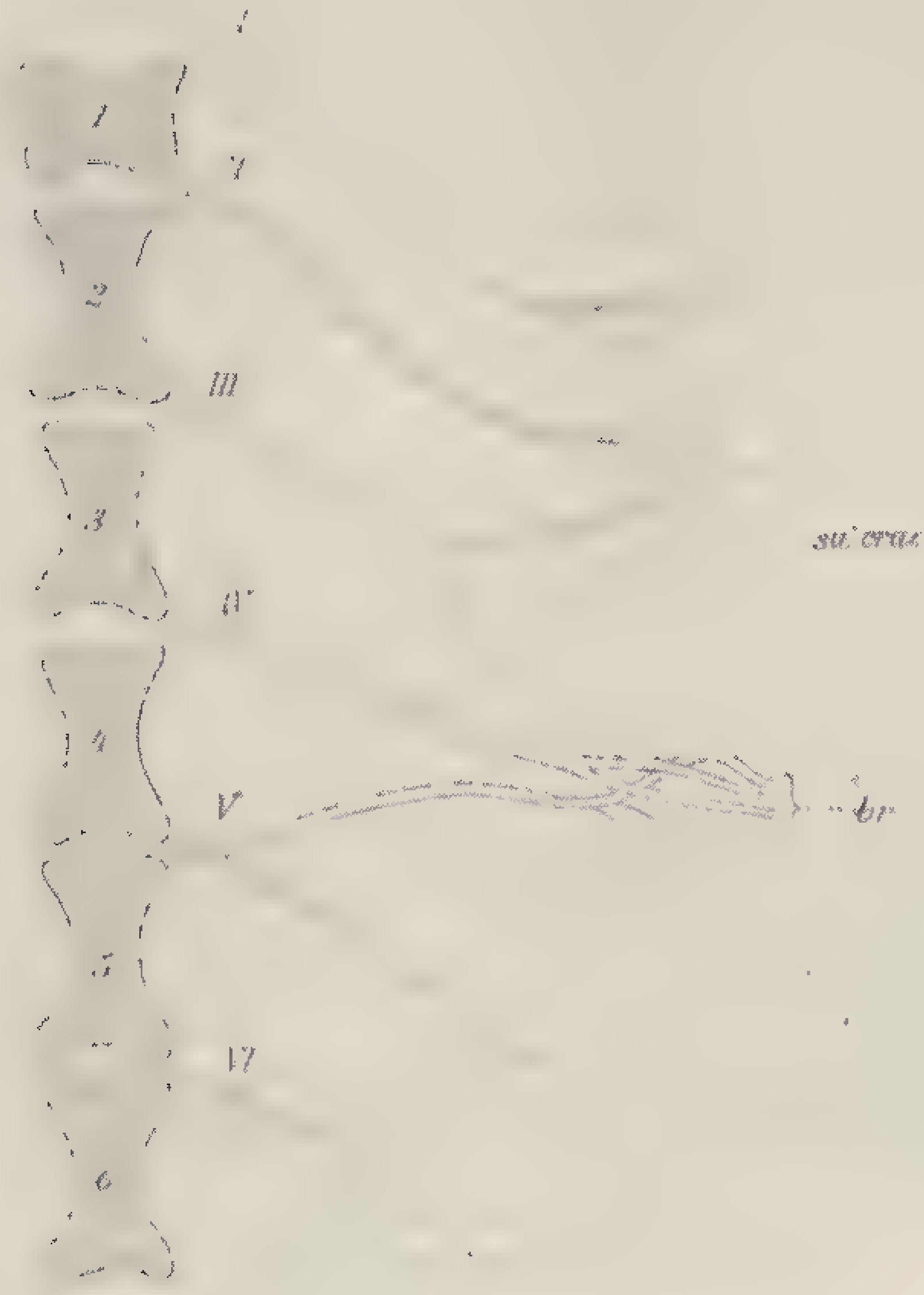
Fig. 1. Diagram showing topography of brachial plexus of left side.

Fig. 2. Diagram of lumbo-sacral plexus of left side, as found in α type, group A.

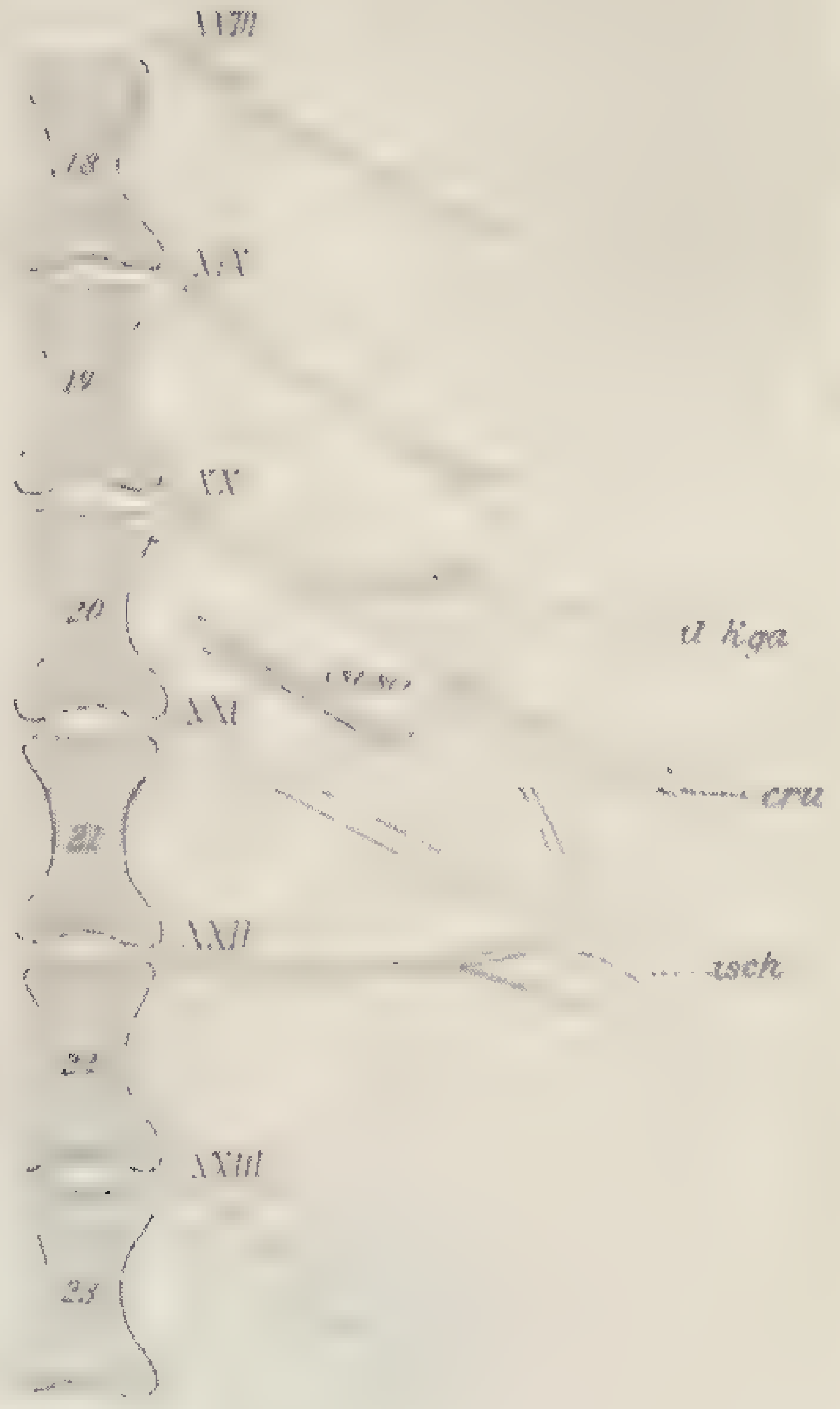
Fig. 3. Diagram of lumbo-sacral plexus of left side, as found in β type, group A.

Fig. 4. Diagram of lumbo-sacral plexus of left side as found in group B.

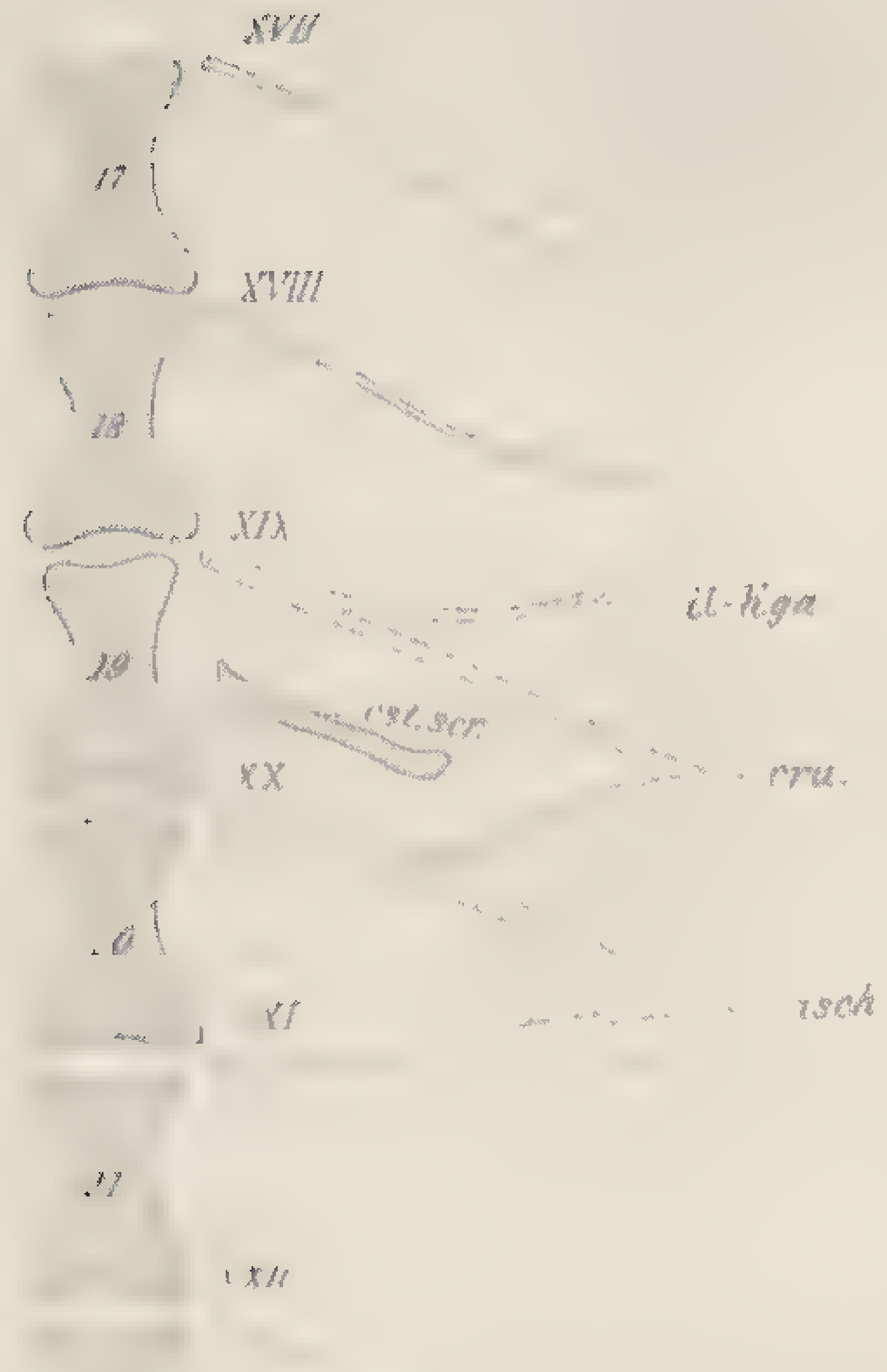
1


I
1
II
2
III
3
su.crau.
IV
4
V
br
5
VI
6

4


XVIII
18
XIX
19
XX
20
il-h.ga
cst.scr.
XXI
21
cru
XXII
isch
22
XXIII
23

2


XVII
17
XVIII
18
XIX
il-h.ga
19
cst.scr.
XX
cru.
XI
isch
21
XII

3

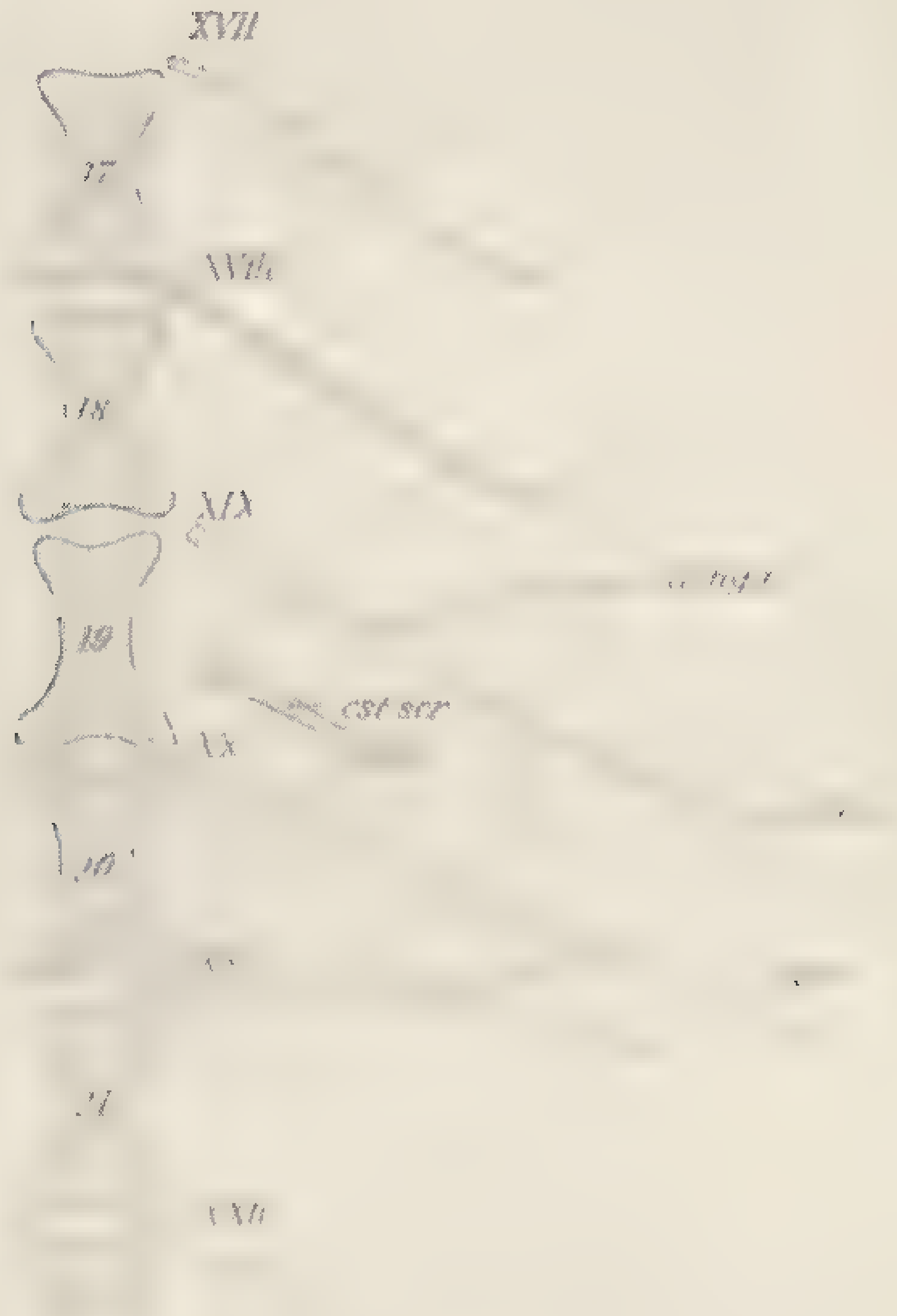

XVII
17
XVIII
18
XIX
19
cst.scr.
XX
21
XXII

PLATE 2.

Fig. 5. Diagram of plexus of both sides in a specimen bearing asymmetrical sacral ribs on vertebræ 19 and 20.

Fig. 6. Diagram of plexus of both sides of a specimen bearing asymmetrical sacral ribs on vertebræ 18 and 19.

Fig. 7. Diagram showing a bifurcate transverse process and sacral rib.

Fig. 8. Diagram of sacrum of a specimen with a supernumerary sacral rib on one side.

Bulletin of the Museum of Comparative Zoölogy

AT HARVARD COLLEGE.

VOL. XXXI. No. 5.

REPORTS ON THE DREDGING OPERATIONS OFF THE WEST COAST OF CENTRAL AMERICA TO THE GALAPAGOS, TO THE WEST COAST OF MEXICO, AND IN THE GULF OF CALIFORNIA, IN CHARGE OF ALEXANDER AGASSIZ, CARRIED ON BY THE U. S. FISH COMMISSION STEAMER "ALBATROSS," DURING 1891, LIEUT. COMMANDER Z. L. TANNER, U. S. N., COMMANDING.

XXII.

THE ISOPODA.

By H. J. HANSEN.

[Published by Permission of MARSHALL McDONALD and J. J. BRICE,
U. S. Fish Commissioners.]

WITH SIX PLATES,
AND A CHART OF THE ROUTE OF THE "ALBATROSS."

CAMBRIDGE, MASS., U. S. A.:
PRINTED FOR THE MUSEUM.
DECEMBER, 1897.

No. 5. — *Reports on the Dredging Operations off the West Coast of Central America to the Galapagos, to the West Coast of Mexico, and in the Gulf of California, in charge of* ALEXANDER AGASSIZ, *carried on by the U. S. Fish Commission Steamer "Albatross," during* 1891, Lieut.-Commander Z. L. TANNER, U. S. N., Commanding.

[Published by permission of MARSHALL McDONALD and J. J. BRICE, U. S. Fish Commissioners.]

XXII.

The Isopoda. By H. J. HANSEN.

THE collection contains in all fifteen species, fourteen of which, all marine, I have considered new to science, while one form — belonging to the Oniscidæ — is terrestrial in habit, and proves to be a well known species. Of the fourteen marine species, eight are free-living forms, and one is parasitic on fishes; these nine species are easily referred to genera established many years ago. The remaining five species belong to the subfamily Bopyrinæ, of the very extensive family Epicaridea; they present several peculiarities in structure, and moreover they are rather interesting since no form of the Bopyrinæ has heretofore been found on truly deep-sea animals. For particulars, however, the reader must be referred to the special description later on.

Besides my special account a few remarks must suffice.[1] Since each of the families is represented by only a few species, I am unable to attempt improvements in the classification of any of them. In a previous paper — Isopoden, Cumaceen und Stomatopoden der Plankton-Expedition (Ergebnisse der Plankton-Expedition der Humboldt-Stiftung, Bd. II. G. c) — I have proposed a partly new arrangement of the Isopoda, with observations on some of the families, and to this treatise the reader must be referred for several particulars. I have thought it useful to illustrate all the species rather fully, and to describe them in some detail, taking into consideration the best representations in the literature, yet altering and adding where it seemed advisable.

---

[1] The Director of the Entomological Department of the Zoölogical Museum in Copenhagen, Inspector Dr. F. Meinert, had commenced to deal with the material, but being engaged in other work, he transferred to me the preparation of this report. Only the following particulars are of interest. He had recognized the two species of Asellota and all the species of Cymothoidæ as new to science; furthermore, he had furnished them with names, and on the labels briefly mentioned the species already published to which each of the new forms was most closely allied. Some of the names and most of these hints on affinity are adopted in the report, which otherwise is wholly a work of my own. Yet it must finally be mentioned that Mr. G. Budde-Lund has determined the single species of Oniscidæ.

ASELLOTA.

Of this large tribe only two species were secured. Both belong to the Munnopsidæ G. O. Sars, a family rather badly limited, and both must be referred to the genus *Eurycope* G. O. Sars. Unfortunately, the material is rather scanty and all the specimens are much mutilated, yet I am able to draw attention to a point of significance, namely, that the genus with the limits still adopted presents startling differences in the structure and shape of the mandibles of some of the species. In the two species here described the mandibles possess distally a cutting portion, behind this a "lacinia mobilis"[1] with a row of setæ on each mandible and a strong "cuspis laciniæ" on the left one, and farther backward a well developed molar process. In the small Norwegian species the mandibles seem to be of similar structure,[2] but in the large *Eurycope gigantea* G. O. Sars they are very different. In this species each mandible has a very long oblique edge on the inner side, the molar process is very short and badly defined, no lacinia mobilis is found, etc. It may be added that the two pairs of jaws also present differences from those in the species to be described here. (The mouth organs of *Eurycope gigantea* were first described by G. O. Sars in the Norwegian North-Atlantic Expedition, Zoöl., Crustacea, Vol. I. pp. 132, 133, Plate XI. Fig. 10–14, and shortly afterwards by the present author in his account of the Crustacea in Dijmphna-Togtets zool.-bot. Udbytte, 1877, pp. 199–201, Tab. XX. Fig. 3*c*–3*g*.) It is interesting to observe that great differences in the structure and armature of the mouth organs are found in species which in general shape and other structural features seem to be rather closely allied. Unfortunately, the mouth parts in several of the species described by Beddard in the "Challenger" Isopoda are entirely unknown.

---

[1] This and the following term are set forth and explained in my paper: Cirolanidæ et Fam. nonn. prop. Musei Haun. (K. Danske Vidensk. Selsk. Skrifter, 6 Række, naturv.-math. Afdeling, V. pp. 239–426, Tab. I.–X.)

[2] At my request, Prof. G. O. Sars very kindly sent me the proof-sheets containing the account of the Munnopsidæ, in his new leading work on the Isopoda. He has divided the family into two families, etc., but he still maintains the genus *Eurycope* in its old and very wide extension, yet remarking that some of the species established by Beddard "ought perhaps more properly to be separated as types of nearly allied genera."

1. **Eurycope pulchra**, n. sp.

Plate I. Fig. 1–1 i.

One much mutilated male and six females, three of them with the marsupium well developed, the others much more than half grown or almost fully grown, were captured.

Head. The dorsal surface with three acute processes, the two anterior of which are rather small, each lying a little behind the antennula, while the third odd process is rather good-sized and separated from the two others by a deep and rather broad furrow. On each side this furrow runs down the lateral surface of the head, above it bends obliquely forward, converging with the furrow from the other side, and finally terminating in a median impression between the two anterior processes. The labrum is very large and prominent, anteriorly rounded.

Antennulæ. The basal joint of the peduncle is oblong, anteriorly cut off; the most distal part of the interior side, where the second joint is articulated, is incised; the upper side is irregularly arched, the distal part of the under side longitudinally somewhat excavated. The second joint is as usual short, the next slender and of about the same breadth at both ends; the anterior inner angle somewhat produced, acute. Third joint somewhat shorter and much more slender than the second. The flagellum somewhat exceeding one third of the length of the body, with innumerable joints.

Antennæ. In no specimen are more than the four proximal short joints and sometimes the basal part of the very elongated fifth joint preserved. Third joint anteriorly on the limit between the exterior and the lower side produced into a very conspicuous acute process; the exopod (squama) very small and quite fused with the third joint, not even set off by a transverse suture (compare the following species).

Mandibles (Fig. 1 *b* and 1 *c*). Of about the same shape as in *Janira* and allied genera. The cutting portion (*a*) compressed, much higher (when seen from in front) than broad, ending with three teeth. Pars molaris (*b*) moderately long, somewhat compressed, so that it is broader when seen from in front than when seen from below as in the figure; distally it is cut off obliquely, with some setæ, and as usual the terminal face of the two molar processes is somewhat differently shaped. Lacinia mobilis (*l*) with numerous setæ, and the cuspis lacinia on the left mandible strongly developed, compressed and much higher than broad, ending in four teeth. The palpus stout, three-jointed, second joint almost double as long as the first; third joint of a peculiar aspect, curved, rather broad, with a conspicuous incision on the anterior margin.

Maxillulæ (Fig. 1 *d*). The lobe (l^1) of the first joint (1) in its distal half rather narrow and curved, with numerous hairs at the rounded apex, but without any spine-like seta. The oblique terminal margin of the lobe (l^3) of the third joint, as in other species, with numerous long spines.

Maxillæ (Fig. 1 *e*). The lobe (l^2) of the second joint proportionally rather narrow, with hairs along the interior margin and on the rounded terminal margin; the two lobes (l^3) of the third joint with some long and robust setæ at the apex.

Maxillipeds (Fig. 1 *f*). Second joint (2) rather long, with about sixteen coupling hooks (*h*) at the inner margin; the terminal margin of its lobe (l^2) coarsely serrated and hairy. Fourth and fifth joints, as in other species, much expanded, but not to such a degree as, for instance, in the following species; the fourth joint conspicuously narrower than the second, and considerably larger than the fifth. Sixth and seventh (7) joints small and slender. The epipod (*ep.*) with a somewhat produced acute angle at the middle of the exterior margin.

Thorax. As usual in this genus, the thorax is divided into two parts, the first of which, consisting of four segments, in this species equals in length the second part. The first segment considerably narrower than the second, the fifth nearly twice as broad as the first. The four anterior segments with a transverse depression in a considerable part of the breadth. The first segment with a single small dorsal process. Second, third, and fourth segments each with a median, very high, laterally compressed, acute dorsal process, turning obliquely forward and rising just behind the anterior margin; besides, the second and third segments with a short rounded protuberance in the median line a little in advance of the posterior margin. The third and the fourth segment with the antero-lateral angle produced into an acute, almost spine-like process; on the first two segments the same angle is rounded. The three posterior segments with a median, longitudinal, rather broad impression, on each side limited by a low keel, anteriorly produced into an acute process, which is long on the fifth and short on the seventh segment. The antero-lateral angle of the three last named segments produced into an acute process, turning forward and somewhat outward, the process being long on the fifth segment, shorter, but almost broader on the last two segments; finally, on the lateral margin a little in advance of the posterior angle, a protuberant rounded process, which is very low on the fifth segment, somewhat larger on the two others, especially on the last one. The whole dorsal surface of the trunk, as of the abdomen, closely set with very small granulations, giving it a faintly scabrous appearance. While the first segment is movably jointed with the head, and the articulation between the four anterior segments, and especially between the fourth and the fifth segment, is very well developed, the three posterior segments are immovably connected with one another and with the abdomen.

Thoracic Legs. The basal joint of the four anterior pairs with the antero-lateral angle produced into a rather good-sized, distally almost spine-like acute process, and laterally with a shorter projecting process; the basal joint of the three posterior pairs smooth. The first pair (Fig. 1 *g*) scarcely of medium length, very slender; the fifth joint almost as long as the second, somewhat curved, very slender, and not expanded on its under side. Of the second, third, and fourth pairs only the two proximal joints are not broken off. In the three last pairs the fifth joint is almost twice as long as broad (Fig. 1 *h*), the seventh joint (7) as long as the fourth, and very slender (in Figure 1 *h* all the hairs are omitted).

Abdomen. As long as the four posterior thoracic segments together, narrower than the seventh segment, and decreasing in breadth from the anterior angle, which is produced into a triangular acute process, turned forward and especially outward. It consists of at least two visible segments — the posterior, of course, consisting of fused segments — fused together, the anterior of which is short; besides, there is seen across the anterior part of the second segment a curved transverse furrow, perhaps indicating a rudiment of a second articulation. In the median line, just behind the furrow between the first segment and the rest of the abdomen, is a small tubercle, especially obvious in a lateral view as a rudimentary process. On the dorsal side are two deep longitudinal furrows, at a considerable distance from each other, and anteriorly curving outward. The posterior margin with three acute processes, the median one curved considerably downward and much larger than the two others, each of which is situated close inside the point where the dorsal furrow reaches the posterior margin. The oblique terminal face of the abdomen is quite similar in both sexes and rather peculiar (Fig. 1 *a* and 1 *i*): the hind margin with the three processes just mentioned, the oblique lateral margin a little arcuate, while the infero-anterior margin is short and concave, the infero-lateral angle being produced into a shorter process; on the upper half of the terminal face are seen the two oblong-triangular anal doors (Fig. 1 *i*, *d*), and just outside each door the uropod is attached. In the female the ventral operculum (the first pair of abdominal limbs) has an impression along with and somewhat inside of the lateral margin and close to the posterior margin; in the median line it possesses a keel, which somewhat before the middle is produced into a rather long, moderately compressed acute process. In the male the operculum (the first and second pairs of abdominal limbs together) is represented in Figure 1 *i*, and scarcely needs a special description. (Having but one male specimen, I omit the description of the "appendix masculina" on the second limb.)

Uropods (Fig. 1 *i*). Each consists of a moderately short and very slender peduncle and two 1-jointed rami, the interior of which is about as long as the peduncle and still more slender, the exterior one somewhat shorter.

Size. A female specimen whose marsupium is still rudimentary (consisting only of small plates on the second and fourth pairs of legs) is 28 mm. long and 11.2 mm. broad. Of the three females with the marsupium completely developed (in two specimens filled with eggs) the largest is a little smaller than the specimen with rudimentary marsupium; the smallest is 23.3 mm. long and 9.8 mm. broad. The youngest female is 20.3 mm. long; the male is about 24.5 mm. long and 10 mm. broad.

Habitat. Station 3361 (Lat. 6° 10′ N., Long. 83° 6′ W.), 1471 fathoms, 2 specimens; Station 3413 (Lat. 2° 34′ N., Long. 92° 6′ W.), 1360 fathoms, 5 specimens.

Remarks. This species is closely allied to *Eurycope fragilis* Bedd. ("Challenger" Isopoda, p. 63, Plate XI. Fig. 8–12); but if the drawings of Beddard are trustworthy in detail, my species is easily distinguished from *E. fragilis* by the processes on the dorsal surface of the head, by the shape of the lateral margin of the three posterior thoracic segments, by the direction of the postero-lateral abdominal processes, etc. However, a thorough revision of many of the "Challenger" Isopoda, especially of the Asellota (sens. lat.), is very much needed.

2. Eurycope scabra, n. sp.

Plate I. Fig. 2–2 *d*; Plate II. Fig. 1.

Only one single and ill-handled female specimen is present; yet I hope that the species can be easily recognized, especially by the aid of my figures.

Head, thorax, and *abdomen* without any processes, and scarcely with sharp angles; but with the exception of a transverse belt across each of the four anterior thoracic segments, the dorsal surface of the body is almost wholly covered with numerous granulations, so that it becomes scabrous in a much higher degree than the preceding species.

Antennulæ. Absent.

Antennæ. Only the four proximal joints are present. The third joint without any process, but above at the exterior side is seen a small triangular and rounded exopod, well set off by a suture.

Mandibles. Only the left mandible (Fig. 2 *a*) has been examined. The cutting portion well developed, ending in five teeth; the lacinia with about six setæ, and the cuspis laciniæ large, with teeth of very different magnitude. The molar process rather long and proportionally slender, seen from below (as in Fig. 2 *a*) almost conical with the end cut off very obliquely; seen from in front the distal part is somewhat broader, and the terminal face is vertical, with sharp serrulation and a few broad hairs; but in the lower end of the face a triangular process is seen, and it is this process which in Figure 2 *a* overlaps the greater part of the end. The palp is very slender; second joint but a little longer than the first; the third very slender.

Maxillulæ (Fig. 2 *b*). The distal part of the lobe of the first joint broader and less curved than in the preceding species, hairy and without spine-like setæ; the lobe of the third joint about as in *Eurycope pulchra.*

Maxillæ (Fig. 2 *c*). The lobe of the second joint distally proportionally narrow and tapering towards the rounded apex, which is furnished with normal hairs.

Maxillipeds (Fig. 2 *d*). Second joint rather elongate, its lobe with the terminal margin closely serrated and with about twelve coupling-hooks at the inner margin. Fourth and fifth joints more expanded than in *Eurycope* *pulchra*, the fifth almost as large as the fourth, and its inner margin partly serrated; sixth and seventh joints much broader than in the preceding species. The epipod with the exterior margin evenly curved.

Thorax. It was badly preserved, and therefore the relative breadth of the segments could not be drawn with so much certainty as could be wished. The want of processes and the scabrous surface are mentioned above. The three posterior segments, without any median dorsal impression not connected immovably with each other, and somewhat shorter than the four others together; the last segment seems to be movably united with the abdomen.

Thoracic Legs. The basal joint of the four anterior pairs anteriorly or exteriorly produced into an angle or short scabrous process. The first pair (Plate II. Fig. 1) rather short and stout; the fifth joint conspicuously shorter than the second, compressed and somewhat expanded on the under side, the margin of which is hairy. Of the six other pairs of legs only the basal joint is preserved.

Abdomen. It is nearly ovate and proportionally large compared with the thorax, but neither shape nor magnitude could be drawn with absolute certainty, as the abdomen was roughly handled. The basal segment is very short; for the rest only a pair of very faint somewhat curved longitudinal impressions are seen on the scabrous dorsal surface. The operculum in the female without any keel.

Uropods. Somewhat longer than in the preceding species, but of about the same shape.

Size. The specimen described is about 25.6 mm. long, and 8.4 mm. broad.

Habitat. Station 3413 (Lat. 2° 34′ N., Long. 92° 6′ W.), 1360 fathoms, 1 specimen.

Remarks. It is easily distinguished from all other large species hitherto known by the general shape of thorax and abdomen, and the want of processes.

CYMOTHOIDÆ.

As to the limitation and the constituent elements of this family I refer to the above named report on the Isopoda of the German Plankton Expedition. Of its six sub-families only two, namely, Æginæ and Cymothoinæ, are represented in the collection, the first sub-family by six, the second by one species. The leading work on these two sub-families is Shiödte and Meinert: Symbolæ ad Monogr. Cymothoarum, Crust. Isopod. Familia (Naturh. Tidsskr., 3 R., Bd. XII.-XIV., 1879–84), and further remarks on the structure of the mouth and the classification are found in my above named work, Cirolanidæ, etc.

In the large genus *Æga* Leach, not rarely several species are closely allied to one another, and three of the four species established here differ only in small features from species living in the most northern part of the Atlantic (in Norway, Greenland, etc.). In the following, some characters derived from the structure of the thoracic legs, and partly overlooked by earlier authors, will be used; besides, the shape of the posterior angles of the thoracic "epimera," of the sixth abdominal segment, and especially of the uropods, furnish us with more distinguishing marks than are generally recognized, but as most of these details are more easily apprehended from figures, I will direct the attention of future students to these facts, believing that proportionally rather large and very accurate drawings of the parts mentioned will be extremely useful.

In specimens of Æginæ taken on fishes, the ventral side of the thorax is often, nay almost generally, vaulted, and sometimes very considerably so, owing to the fact that the alimentary canal is greatly distended by blood sucked from the host; another result of this swollen condition is that the segments of the thorax very often become drawn out from each other. In specimens taken on the bottom of the sea by trawl or dredge, the ventral side is not vaulted, and the thoracic segments are not drawn out, it follows that such specimens are comparatively shorter in proportion to their breadth than most of the specimens taken on fishes, and therefore present a somewhat different aspect. No specimen of the Æginæ in this collection has the ventral side vaulted, and all seem to be taken on the bottom.

Schiödte and Meinert divide the species of the genus *Æga* into two groups. The first of them is thus diagnosed: "Scapi antennarum infra plani vel concavi, invicem accommodati. Lamina frontalis plana vel concava," and to this group the two first described species, *Æ. maxima*, n. sp., and *Æ. acuminata*, n. sp., must be referred. To the other group the two authors ascribe the following characters: "Scapi antennarum teretiusculi vel compressi, invicem liberi. Lamina frontalis convexa vel compresse elevata," and to this belong the two other species, *Æ. plebeia*, n. sp., and *Æ. longicornis*, n. sp.

3. Æga maxima, n. sp.

Plate II. Fig. 2–2 *c*.

Only one specimen, a female without marsupium.

Head. The frontal margin rather concave on each side; the median elongation acute, reaching to about the middle of the interior margin of the first joint of the antennulæ. The frontal plate "lamina frontalis" (on the ventral side of the head), about as long as broad, seen as much as possible from the side considerably convex, and seen from in front with a low and rather broad sublateral carina, and somewhat excavated in the middle. The eyes ovate, the shortest distance between them only a little less than the basal joints of both antennulæ together.

Antennulæ. Reaching very little beyond the end of the peduncle of the antennæ, and a little beyond the anterior angle of the first thoracic segment. The peduncle very little longer than the flagellum; its basal joint as long as broad, with the upper side flatly convex, and the antero-interior angle rectangular. The flagellum 17-jointed.

Antennæ. Each antenna, when bent backward, nearly attains the posterior margin of the second thoracic segment. The proportion between the peduncle and the flagellum is about that of 3 to 5; the flagellum 23-jointed.

Thorax (Fig. 2 *a*). The posterior angle of the first segment rectangular, scarcely produced. For practical reasons, the "epimera" of the six following segments, though in reality constituting the first joint of the legs, are here treated as belonging to the thorax; the epimera of the second thoracic segment with the posterior free angle nearly rectangular, those of the third segment somewhat obtuse-angular. The epimera of the four posterior segments posteriorly considerably produced; those of the fourth and fifth segments posteriorly obliquely rounded; the last two pairs with the triangular apex a little rounded.

Thoracic Legs. All clumsy. In the three anterior pairs the fourth joint (the epimeron considered as the first joint) is shorter than the third, considerably incrassated, in the first pair with only one spine, in the second with six or seven (Fig. 2 *b*), in the third with nine short spines at the interior margin; the fifth joint only in the third pair with a spine at the antero-interior angle; the sixth joint short, without keel on the inner side; the claw (consisting of the seventh joint fused with the real claw) short and robust. The four posterior pairs (Fig. 2 *c*) with numerous, comparatively short spines.

Abdomen. The first segment partly free, a little broader than the fourth. The sixth segment about 1½ times broader than long; the dorsal surface feebly convex, very slightly keeled in the median line, and between this keel and the base of the uropod is seen a large, but shallow depression; as the posterior apex unfortunately is broken off, nothing can be said about its shape, but most likely it was acute, and the posterior margin probably with about five spines on each side.

Uropods. They reach a little beyond the end of the abdomen; both rami are proportionally narrow, of the same breadth and the same length, the inner ramus therefore posteriorly surpassing the outer one. The inner ramus more than three times longer than broad; the interior margin from a point a little behind the apex of the very long and narrow process from the peduncle turning obliquely outward, thus forming a posterior margin, with five or six small spines; the exterior margin somewhat convex, but at a short distance from the rounded tip of the branch it changes its direction, bending somewhat outward, thus forming a low incision. The outer ramus with the tip rounded; the distal part of both margins faintly serrated with a smaller number of spines.

Color. The whole dorsal surface yellowish white, the eyes grayish.

Size. The single specimen measures 55 mm. in length and 26 mm. in breadth.

Habitat. Station 3362 (Lat. 5° 56′ N., Long. 85° 10′ 30″ W.), 1175 fathoms, 1 specimen.

Remarks. The species is closely allied to *Æ. psora* (L.), but is easily distinguished by its enormous size, and the following characters: a different shape of the frontal plate; the eyes smaller and more distant from each other; the dorsal surface of the last abdominal segment slightly convex, with two large depressions.

4. **Æga acuminata**, n. sp.

Plate II. Fig. 3–3 *b*.

Only one specimen, a female without marsupium.

Head. The frontal margin scarcely as concave on each side as in *Æ. maxima*, the median elongation not reaching the middle of the interior margin of the first joint of the antennulæ. The frontal plate conspicuously broader than long, seen from the side shaped as in the preceding species, seen from in front somewhat concave with projecting lateral margins. The eyes as in the preceding species.

Antennulæ (Fig. 3). Reaching considerably beyond the peduncle of the antennæ, to the middle of the first thoracic segment. The peduncle slightly shorter than the flagellum; the basal joint, seen from in front, quite as broad as long; the dorsal surface somewhat convex; the antero-interior angle a little produced, acute-angled. The flagellum 18-jointed.

Antennæ. When reflexed, reaching to the posterior margin of the second thoracic segment. The relation of the peduncle to the flagellum is about that of 2 to 3; the flagellum 19–20-jointed.

Thorax (Fig. 3 *a*). The posterior margin of the epimera of the second to the fifth segment and the corresponding margin of the first segment sinuate, being directed a little forward just inside the somewhat produced postero-lateral angle, which is scarcely rectangular, but a little acute-angled. The epimera of the sixth segment forming a transition between those of the fifth and of the seventh segment, the last named pair posteriorly and laterally considerably produced and acute.

Thoracic Legs. They are robust, though scarcely as clumsy as in *Æ. maxima*, but very similar in shape and armature. In the three anterior pairs the claw is somewhat longer; the thick fourth joint in the first pair with one spine, in the second with five, in the third with six to eight spines. The spines on the four posterior pairs scarcely as numerous as in the preceding species, but somewhat longer.

Abdomen. The first segment almost totally covered, very conspicuously broader than the fourth. The last segment scarcely 1⅓ times broader than long (in Fig. 3 *b* it seems to be proportionally broader, owing to the circumstance that the figure presents the projection of the posterior segments); posteriorly it is considerably produced, acute, with about three spines on each side of the tip; the dorsal surface is rather convex, median keel and sublateral depressions scarcely visible.

Uropods (Fig. 3 *b*). Much as in *Æ. maxima*, so that only the more essential differences will be pointed out. The outer ramus reaching a little beyond the inner one; the inner ramus is more deeply incised on the exterior side, and the posterior margin is somewhat longer: thus we obtain a distal part forming an obtuse angle with the larger proximal part.

Color. The dorsal surface is light yellowish gray with a faint purple tone on a part of the three anterior thoracic segments, and the last abdominal segment yellowish white; the eyes dark grayish, almost black.

Size. The single specimen is 31 mm. long, 16.2 mm. broad.

Habitat. Station 3403 (Lat. 0° 58′ 30″ S., Long. 89° 17′ W.), 384 fathoms, 1 specimen.

Remarks. The species is very closely allied to *Æ. psora* (L.), but is distinguished especially by smaller eyes, longer antennulæ, and the last abdominal segment being posteriorly more produced. From *Æ. maxima* it is distinguished especially by longer antennulæ, and by a different shape of the last abdominal segment and of the uropods.

5. Æga plebeia, n. sp.

Plate II. Fig. 4–4 *d*.

Six specimens, one male and five females, three of the latter with well developed marsupium.

Head. The frontal margin with the sub-median curves rather indistinct; the median process extends a little below the inferior edge of the antennulæ, its apex almost or quite reaching the frontal plate. The frontal plate about twice as broad as long and strongly compressed, forming a high tranverse keel, which, seen from in front, shows the shape of the half of an oval. The eyes (Fig. 4) are very large; the distance between them considerably shorter than the breadth of the frontal process.

Antennulæ. Much longer than the peduncle of the antennæ (Fig. 4), and bent backwards, reaching almost to or even beyond the posterior angle of the first thoracic segment. The peduncle is somewhat shorter than the flagellum, and almost attains the distal end of the penultimate joint of the peduncle of the antennæ; the first joint is about as long as broad, with the antero-interior angle broadly rounded; the third joint of the peduncle as long as, or a little longer than, the two proximal joints together. The flagellum with twenty-one to twenty-three joints.

Antennæ. They reach a little beyond the posterior margin of the second, or almost to the posterior margin of the third thoracic segment. The flagellum 1⅓ or 1½ times longer than the peduncle, with seventeen or eighteen joints.

Thorax (Fig. 4 *a*). The postero-lateral angle of the first segment rectangular or a little acute, that of the epimera of the second and generally of the third segment conspicuously produced and acute; the angle of the fifth and sixth epimera almost or quite rectangular. The epimera of the seventh segment somewhat produced and acute.

Thoracic Legs. The three anterior pairs slender and rather long: the fourth joint not incrassated, with concave interior margin (Fig. 4 *b*), and with a couple of small spines at the distal inner angle; the sixth joint rather long, with a strong spine on the interior margin near the end; the claw very long, and longer than the sixth joint. The four posterior pairs are slender; the fourth joint elongate, and considerably longer than the fifth.

Abdomen. The first segment partly covered, very conspicuously broader than the fourth. The last segment (Fig. 4 *d*) 1¼ times broader than long; the tip acute, but scarcely produced; the posterior margin with six to eight small serratures, with scarcely visible spines on each side of the apex; the dorsal surface slightly convex, the faint median keel and the sub-lateral impressions almost as in *Æ. maxima* (see *supra*).

Uropods (Fig. 4 *d*). They reach somewhat beyond the apex of the abdomen, the outer ramus almost or quite attaining the end of the inner one. The inner ramus relatively broad, scarcely half as broad as long, of a somewhat triangular shape; the posterior margin considerably shorter than the antero-interior one, with seven or eight rather fine serratures; the exterior margin with a break at some distance from the acute tip, and two or three serratures between the tip and the break, the rest of the margin almost straight and smooth. The outer ramus is conspicuously narrower than the inner, yet rather broad, the apex acute, not produced.

Color. The dorsal surface yellowish white, the eyes gray, somewhat blackish.

Size. The largest specimen, a female with marsupium, is 37 mm. long and 17 mm. broad; the smallest female with marsupium is but 22 mm. long; the single male is 23.4 mm. long and 10.5 mm. broad.

Habitat. Station 3363 (Lat. 5° 43′ N., Long. 85° 50′ W.), 978 fathoms, 4 specimens; Station 3371 (Lat. 5° 26′ 20″ N., Long. 86° 55′ W.), 770 fathoms, 1 specimen; Station 3402 (Lat. 0° 57′ 30″ S., Long. 89° 3′ 30″ W.), 421 fathoms, 1 specimen.

Remarks. The species is closely allied to *Æ. ventrosa* M. Sars, but in the last named species the frontal plate is lower and of another shape, the eyes are more narrow, not occupying so much of the dorsal surface of the head, the epimera of the sixth, and especially those of the seventh segment are considerably more produced, and the outer ramus of the uropods is somewhat broader.

6. **Ægа longicornis**, n. sp.

Plate II. Fig. 5-5 *b*; Plate III. Fig. 1-1 *a*.

Only one specimen, a female without marsupium.

Head. The frontal margin with the sub-median curves rather faint; the median process as in the preceding species. The frontal plate forms a very high transverse keel, which, when the head is seen from in front, protrudes strongly beyond the basal parts of the antennulæ and the antennæ, and has a straight inferior margin and rounded lateral angles. The eyes (Fig. 5) comparatively narrow, the shortest distance between them a little shorter than the basal joint of both antennulæ and the breadth of the frontal process together.

Antennulæ. They reach considerably beyond the peduncle of the antennæ, and almost to the postero-lateral angle of the first thoracic segment. The peduncle a little shorter than the flagellum; its basal joint about as long as broad, with the antero-interior angle broadly rounded, the third joint scarcely shorter than the two proximal joints together. The flagellum with about fifteen joints.

Antennæ. They are unusually long, reaching to the middle of the fifth thoracic segment. The flagellum more than twice as long as the peduncle, with twenty-two joints.

Thorax. The postero-lateral angle of the first segment and of the epimera of all the other segments acute and more or less acute-angled (Fig. 5 *a*).

Thoracic Legs. The three anterior pairs are slender and rather long (Plate III. Fig. 1); their fourth joint scarcely incrassated, with concave inner margin, and in the second and third pairs with a couple of spines at the distal inner angle; the sixth joint rather long and without spines; the claw rather long, but scarcely longer than the sixth joint. The four posterior pairs rather long and slender (Plate III. Fig. 1 *a*); the fourth joint a little shorter, or at all events not longer, than the fifth.

Abdomen. The first segment almost covered, and very conspicuously broader than the fourth. The last segment (Fig. 5 *b*) about $1\frac{1}{3}$ times broader than long; the apex acute but very little produced; the posterior margin on each side of the apex with four or five comparatively coarse serratures, and a conspicuous spine in each incision; the dorsal surface very flatly convex, with a transverse depression near the base and the median keel not discernible.

Uropods (Fig. 5 *b*). They reach far beyond the apex of the abdomen, the inner ramus scarcely attaining the end of the outer one. The inner ramus is relatively broad, but yet more than twice as long as broad, triangular, the triangle being almost isosceles, with rounded vertex, as the posterior margin is almost as long as the antero-interior one; the exterior margin almost straight, with about five coarse serratures in the distal half, and the posterior margin is also serrated; the apex is acute. The outer ramus much narrower than the inner one, about four times longer than broad; the apex much produced, acute.

Color. The dorsal surface is yellowish white, the eyes black.

Size. The single specimen is 14.5 mm. long and 7.5 mm. broad.

Habitat. Station 3402 (Lat. 0° 57′ 30″ S., Long. 89° 3′ 30″ W.), 421 fathoms, 1 specimen.

Remarks. The species is easily distinguished by the following characters together: the long distance between the eyes, the long antennæ, and the relative length of the rami of the uropods.

7. **Rocinela laticauda**, n. sp.

Plate III. Fig. 2–2 *e*.

Three specimens of very different size, one a large and in all probability adult male; no female with marsupium.

Head.[1] The eyes of medium size, the shortest distance between them about as long as the last joint of the peduncle of the antennæ; the distance in the smallest specimen is comparatively a little shorter than in the largest one.

Antennulæ. They surpass a little the middle of the last joint of the peduncle of the antennæ (Fig. 2 *a*); the peduncle reaching a little beyond the extero-anterior angle of the third joint of the peduncle of the antennæ; the flagellum in the small specimen with five, in the large specimens with six joints.

Antennæ. They reach a little beyond the middle of the third thoracic segment; the flagellum in the small specimen with fifteen, in the two other specimens with sixteen joints.

Thorax. The epimera (Fig. 2 *b*) of second and third thoracic segments posteriorly rounded and not produced, those of the fourth segment somewhat produced with rounded apex, those of the three posterior segments considerably produced and almost acute.

Thoracic Legs. The three anterior pairs (Fig. 2 *c*) tolerably stout: the fourth joint with about four acute spines, some of them rather long; the sixth joint quite as broad as the fourth, its large and broad expansion on the inner side with six spines. The four posterior pairs (Fig. 2 *d*) with numerous slender spines.

Abdomen (Fig. 2 *e*). The first segment is entirely concealed under the last thoracic one. The abdomen increases very conspicuously in breadth from the second to the fourth segment. The last segment is large and broad, posteriorly very broadly rounded; the dorsal surface is keeled anteriorly in the middle, and from the keel towards the lateral margin it is rather deeply, or, in the two smaller specimens, deeply and broadly depressed, the depression not reaching the lateral margin; the posterior margin with a number of very small spines.

Uropods (Fig. 2 *e*). They surpass a little the last abdominal segment. The outer ramus reaches very little beyond the inner one, is considerably, but not 1½ times, broader than this, and is furnished with a number of spines on a larger part of its exterior margin. The inner ramus with spines on the terminal margin, and on the larger part of the outer margin.

---

[1] Schiödte and Meinert write (Nat. Tidsskr., 3 R., Bd. XII. p. 383) on the species of the genus *Rocinela*: "Bene recordari debet, discrimen, quod individua speciei unius ejusdemque quoad figuram frontis atque sculpturam partis prioris trunci præbent, non sexum, sed ætatem diversam notare." This observation is a very valuable one, as the differences in the front sometimes lead to great confusion. The frontal plate seems to be very small in all species; the thoracic epimera show much smaller differences in the various species than in the species of *Æga*.

Color. The two smaller specimens yellowish white, with a reddish tone on a part of the three anterior segments, and the eyes blackish; the large specimen is more grayish, posteriorly on the dorsal surface of the last abdominal segment and on a part of the uropods reddish brown, the eyes black.

Size. The largest specimen, a male, is 40.5 mm. long, and 16 mm. broad; the two other specimens are immature females, the smallest of them 21 mm. long.

Habitat. Station 3418 (Lat. 16° 33′ N., Long. 99° 52′ 30″ W.), 660 fathoms, 1 specimen; Station 3425 (Lat. 21° 19′ N., Long. 106° 24′ W.), 680 fathoms, 1 specimen; Station 3430 (Lat. 23° 16′ N., Long. 107° 31′ W.), 852 fathoms, 1 specimen.

Remarks. The species is closely allied to *R. australis* Sch. & Mein., but in this last species the eyes are very conspicuously larger and the distance between them considerably shorter than the last joint of the peduncle of the antennæ, the abdomen does not increase in breadth from the base to the fourth segment, the last abdominal segment is somewhat smaller and the outer ramus of the uropods much broader, about 1⅔ times broader than the inner ramus.

8. **Rocinela modesta,** n. sp.

Plate III. Fig. 3–3 c.

Only one somewhat mutilated specimen, a female with marsupium.

Head. The eyes are rather small, occupying only about half of the lateral margin of the head, and the distance between them considerably longer than the last joint of the peduncle of the antennæ.

Antennulæ (Fig. 3). Comparatively long, reaching very little beyond the peduncle of the antennæ. The peduncle surpasses the middle of the penultimate joint of the peduncle of the antennæ. The flagellum with six joints.

Antennæ. In my single specimen only the peduncles are present.

Thorax. The epimera essentially as in the preceding species, yet posteriorly a little more produced.

Thoracic Legs. The first three pairs (Fig. 3 *a*) of medium size, rather slender: the fourth joint with from three to four blunt spines; the sixth joint not as broad as the fourth, the expansion on the inner side rather low and short, with four feeble spines. The four posterior pairs (Fig. 3 *b*) nearly as in the preceding species, but the spines are less numerous.

Abdomen (Fig. 3 *c*). The first segment is completely covered; the second quite as broad as the fourth. The last segment is smaller than in the preceding species, decreasing considerably in breadth from before the middle backward; posteriorly it is comparatively rather narrow and rounded, with some few fine spines on each side of the median line; the dorsal surface is somewhat convex, keeled anteriorly in the median line and with a rather deep but not broad depression from that keel outwards almost to the lateral margin.

Uropods (Fig. 3 *c*). The inner ramus surpasses a little the abdomen and very little the outer ramus, which is somewhat broader than the other; both rami with rather feeble spines on the major part of the exterior margin ; the inner ramus with some spines on the obliquely rounded terminal margin.

Color. The dorsal surface is whitish, the eyes dark.

Size. The single specimen, a female with marsupium, is 23.5 mm. long, and 10.7 mm. broad.

Habitat. Station 3384 (Lat. 7° 31′ 30″ N., Long. 79° 14′ W.), 458 fathoms, 1 specimen.

Remarks. This species is closely allied to *R. maculata* Sch. & Mein., but it totally lacks the four large black spots ; furthermore, in the last named species the uropods are a little shorter and broader, and the two rami of equal breadth, while the outer ramus is conspicuously shorter than the inner one ; the three anterior pairs of legs are relatively shorter and more clumsy, etc.

9. Irona foveolata, n. sp.

Plate III. Fig. 4–4 *b*.

Seven specimens, all females with marsupium, were secured. The species certainly must be referred to the genus *Irona* Sch. & Mein., but as in my opinion it would be of little value to work out a long and very detailed account, I prefer to give a shorter description, especially pointing out the features by which it is distinguished from the four species described by Schiödte and Meinert in their monograph (Nat. Tidsskr., 3 R., Bd. XIV. pp. 383–395), and more particularly from *Irona melanosticta* Sch. & Mein., to which it is rather closely allied. As in adult females of other species belonging to *Irona*, *Lironeca*, etc., the body is unsymmetrical and somewhat variable in shape, in some specimens being contorted to the right, in others to the left side ; furthermore, the last abdominal segment is sometimes as large as shown in the drawing (Fig. 4), sometimes a little larger or smaller, in the smallest specimen even conspicuously smaller.

The body is about twice as long as broad, in the smallest specimen a little shorter and broader, much depressed, but the dorsal surface of the thorax and the median part of the five anterior abdominal segments yet more or less but never strongly vaulted, while the lateral part of the abdominal segments mentioned and the whole sixth abdominal segment are nearly or quite flat, but sometimes obviously contorted.

Thorax. The epimera of the second, third, and fourth thoracic segments are very narrow, seen from above ; those of the fifth segment a little broader and posteriorly more produced. The epimera of the sixth and especially of the seventh segment are much broader and posteriorly much more produced than the others, besides on each side rising considerably above the more lateral part of the dorsal surface of the thorax, which is brought about by the curious fact that these epimera are turned outwards and somewhat upwards.

Abdomen. All the segments are very broad. The last segment either rather thin and tolerably large, or mostly, as in Figure 4, thin and very large, and in this instance almost membranous, so that the marginal part easily becomes folded. The dorsal surface of this last segment sometimes with tolerably distinct, sometimes with very faint median keel, and else almost all over finely and densely pock-marked by exceedingly numerous and very small depressions. (This structure is not clearly defined on the copperplate, as the depressions are far more numerous than in the figure, and the intervals form a kind of irregular reticular work.)

Uropods. They have a very depressed peduncle and thin rami; the outer ramus is oblong-ovate, distally rounded; the inner ramus is considerably longer than the outer, with sub-acute end.

Color. In the six larger specimens the head, the thorax, the five short abdominal segments, and the basal part of the sixth segment, are yellowish with innumerable dark dots; the epimera of the three, and especially of the two, posterior thoracic segments, and the lateral angles of the five anterior abdominal segments are white; almost the whole last abdominal segment is grayish. In the smallest specimen the dorsal surface is darker, more grayish, with exception of the two last pairs of thoracic epimera and the angles of the five anterior abdominal segments, which are white.

Size. The largest specimen is 20.5 mm. long, and 10.5 mm. broad; the smallest is 14.5 mm. long, and 8.2 mm. broad.

Habitat. Station 3355 (Lat. 7° 12′ 20″ N., Long. 80° 55′ W.), 182 fathoms, 2 specimens; Station 3389 (Lat. 7° 16′ 45″ N., Long. 79° 56′ 30″ W.), 210 fathoms, 4 specimens; Station 3391 (Lat. 7° 33′ 40″ N., Long. 79° 43′ 20″ W.), 153 fathoms, 1 specimen. On the labels I do not find any mention of the name or names of the fishes on which the parasites must have been found.

Remarks. The species seems to be well distinguished, especially by the pock-marked surface of the last abdominal segment. No males were found. In the marsupium of one female I found "pullus stadii primi" of Schiödte and Meinert; in Figure *4 a* a leg of the second pair, and in Figure 4 *b* the posterior abdominal segments and the uropods of one of the specimens are shown. This may be sufficient, as the young one in this stage is very similar to those of the genus *Lironeca* drawn by Schiödte. Unfortunately, the "pullus stadii secundi," always much more interesting, was not found.

EPICARIDEA.

As to the division of this very rich and highly interesting family into sub-families the reader is referred to my above mentioned treatise on the Isopoda of the Plankton Expedition. Of the four sub-families admitted (the very doubtful Microniscinæ not included) only one, viz. the Bopyrinæ, is represented in the collection. Of the five species secured both female and male — but no young ones — are present of the four species, while the fifth species is represented only by a male and a small portion of a female.

It is a rather unpleasant task to describe a few new forms of the Bopyrinæ. Most of the authors who have contributed to the knowledge of the group possessed very few species, and often even very few specimens, and the animals being not very easy to examine, and still less to describe and draw, the result is that most of the species are imperfectly represented, and many of the genera badly or not at all limited. Giard and Bonnier have given full descriptions of a few species only, as their principal work on this sub-family has not yet been published. They have made an attempt to divide the Bopyrinæ into three groups, Phyxiens, Bopyriens, and Ioniens; but I am unable to perceive the limits between the two first named groups, and even the group Ioniens is not very sharply defined. We must wait until a number of still unknown forms have been thoroughly studied and many of the already established species reexamined before it will be possible to divide the sub-family into natural groups. I must add, however, that the few descriptions just mentioned of the two authors have been very useful to me. In 1893, T. R. R. Stebbing, in his well known work, "A History of Crustacea — Recent Malacostraca," gave a very good catalogue of all the twenty-one genera and almost all the species hitherto established.

I must confess that I have been unable to refer more than one of my five new species to any of the genera hitherto established, and as they are very different from one another it is necessary to institute four new genera, — a result with which I am rather dissatisfied, not being sure that they all will prove to be valid. On account of the present state of things, I do not venture to lay down diagnoses of the new genera; but I hope that by means of my rather numerous figures and tolerably full descriptions it will be easy not only to recognize my species, but also to place the genera properly and work out the diagnoses, when in the future we get a real systematic arrangement.

10. Cryptione elongata, n. gen., n. sp.

Plate III. Fig. 5-5 *a*; Plate IV. Fig. 1-1 *g*.

A fine female with its male (Fig. 1 *a*, *m*) was discovered.

a. *Female.*

The body is elongate (Fig. 1) and (the uropods not included) about twice as long as broad; the greatest breadth at about the middle.

Head. It forms, when seen from above (Fig. 1), almost a regular transverse oval, with the anterior half projecting in advance of the antero-lateral part of the thorax and the frontal margin considerably and evenly curved; the dorsal surface somewhat convex, with a depression a little inside of the anterior margin. The antennulæ (Fig. 1 *b*, *a*) rather distant from each other, of medium size, 3-jointed; the basal joint is considerably enlarged, the terminal joint minute. The antennæ (*b*) rather long, 3-jointed; the basal joint very large, ovate, with the second joint proceeding from the extero-anterior part; the second joint relatively rather long and robust (compare the following forms), the third somewhat shorter and considerably more slender. A frontal plate is absent, and between the antennulæ, the antennæ, and the labrum is found a rather large free space. The labrum (*c*) is tolerably small, a little broader than the hypopharynx, the posterior margin emarginate. The hypopharynx (*h*) with the lateral margins sub-parallel. Mandibles (*d*), maxillulæ (*e*), and maxillæ (*f*) scarcely need special mention, their general shape and position being easily seen in Fig. 1 *b*. In this figure the place of attachment of the maxillipeds is lettered with *g*. The left maxilliped, seen from below, is shown in Figure 1 *c*; the first joint (1) with its usual free posterior dilatation, the second joint (2) with the exterior dilatation (d^2) which is of secondary origin — as in the females of the family Cymothoidæ — and cannot be considered as an exopod; the palp (*p*) is longer than in the following forms, but not distinctly jointed. The peculiar border behind the attachment of the maxillipeds is well developed, having on each side two oblique, good-sized rather broad, but not long, somewhat fleshy, lamellar processes (Fig. 1 *b*, *l*).

Thorax. On the four anterior segments the ovarian bosses are well developed, occupying but a little more than half the length of the sub-marginal part of each segment; in the other segments the bosses are wanting. The pleural plates ("lames pleurales" of Giard and Bonnier) of the four anterior segments are interesting: each of them is divided by a deep incision into two portions, the anterior of which is oblong, set off by a furrow and especially on the right side of the animal incised or emarginate exteriorly, while the posterior forms a shorter, rounded, not defined lobe. In the three posterior segments the pleural plates are larger and laterally more prominent, but neither divided nor set off. The ventral side of the two posterior segments is elevated and divided by numerous longitudinal ridges into low fleshy lamellæ; the other segments possess a similar, but more narrow, transverse keel divided into small protuberances. The legs are normal, each sitting on an eminence which often is rather prominent (its appearance on the left side of the figure conveys the impression that the leg has a short basal joint, which of course is not the case); the second joint (basipodite, Giard and Bonnier, the basal joint being fused with the segment) not expanded; the claw is present, and none of the joints with keels or rugosities. The first left leg with its marsupial plate is exhibited in Figure 1 *d*, which, better than a long description, will show the differences between the plate in this and in the following forms; the transverse furrow on its exterior side is plainly seen, and on the inner side is found a transverse keel, the proximal part of which is divided into a few lamellæ. The margins of the marsupial plates are more or less hairy; on the anterior margins of all plates the hairs are fewer and rather rudimentary, while especially the inner and posterior margin of the two posterior pairs of plates is densely set with rather short hairs (omitted in Fig. 1 *a*). (The marsupium was empty.)

Abdomen. The segments are distinctly separated on the dorsal side. The five anterior segments, all comparatively broad, on each side produced as good-sized free plates, which mostly are cut off in a more or less oblique direction; on the left side all these pleural plates are bent obliquely upwards. The ventral side of these segments shows a similar but less regular division into low lamellæ as that of the posterior thoracic segments. The pleopods of medium size, each with two subequal rami, the basal part of which is thicker, somewhat fleshy, the distal part more lamellar; some of the rami are oblong-triangular and distally almost produced, others are distally broader and rounded; almost the whole, or at least the major basal part of the ventral surface of all rami is furnished with conspicuous rounded knots, some of which plainly show that this structure is a rudimentary ramification; the pleopods decrease somewhat in size from before backward. Each uropod (Fig. 1) is an oblong, glabrous lamella, which is as large as, or a little larger than, a ramus of the first pleopod.

Size. From the front to the apex of the longest uropod the specimen is 13 mm., and to the end of the last abdominal segment 11.2 mm.; it is 6.6 mm. broad.

b. *Male.*

The body is very elongate, about $3\frac{1}{2}$ times longer than broad (Fig. 1 *e* and 1 *f*).

Head. It is completely fused with the first thoracic segment. The eyes are very small, light grayish, and scarcely visible when the animal is seen from above. The frontal part bends much downward and forms a high border, which covers the basal part of the antennulæ and the antennæ (Fig. 1 *g*); the margin is rather slightly curved. The antennulæ tolerably short, 3-jointed; the basal joint longer and very much thicker than the second; the third joint very slender and rather short. The antennæ rather long, 8-jointed; the first joint a little longer and about twice as broad as the second, which is about as long as, and much thicker than, the third and especially the fourth; the four distal joints exceedingly small. The mouth conical and protruding, but it was utterly impossible to study its elements with any certainty without a dissection.

Thorax. The segments, when seen from above, with their lateral outline feebly rounded and the incisions between them short. Each segment with a median, rather high, basally very broad and distally rounded cone on the ventral side (Fig. 1 *f*); this cone is smaller on the two first segments than on the others. A leg of the first pair is shown in Plate III. Figure 5, and the corresponding leg of the fifth pair in Figure 5 *a*; the general shape and the armature of the fifth and the sixth joint — the first joint as usual fused with the thorax and consequently not drawn — are easily seen.

Abdomen. It occupies one third of the total length, and decreases posteriorly very little in breadth. The six segments are all well separated from each other. The five anterior segments with the lateral part almost triangular, when seen from above; each with a ventral cone as those in the thoracic segments, and, besides, each pleopod is developed as a protuberance of considerable size and directed obliquely inward and a little backward. The sixth segment relatively broad, on each side with a large, narrow conical, obtuse process, probably the uropod, originating from the side and directed somewhat outward and much backward; the posterior margin of the segment is angular.

Size. It is 4.1 mm. long to the apex of the uropods.

Habitat. The described pair were found in the branchial cavity of a specimen of *Nematocarcinus agassizii* Fax., from Station 3407 (Lat. 0° 4′ S., Long. 90° 24′ 30″ W.), 885 fathoms. The swelling of the carapace is oblong, and not very high.

11. Munidion princeps, n. gen., n. sp.

Plate IV. Fig. 2-2 *e*; Plate V. Fig. 1-1 *d*.

Two females with their males were secured.

a. *Female.*

The body, when seen from above (Fig. 1), of an almost pyriform outline, and not quite 1½ times longer than broad (the uropods not included). One specimen has the right margin convex, — a "right" specimen; the other is a "left" specimen.

Head. It is much broader than long and encircled posteriorly and on the major part of its sides of the first thoracic segment; the dorsal surface is somewhat convex, and the frontal border tolerably broad and bent conspicuously upward; the anterior margin is slightly convex. The antennulæ (Plate IV. Fig. 2) separated by a frontal plate; they are of medium size, 13-jointed; the basal joint is comparatively large, the third extremely small. The antennæ are rather short, 3-jointed; the basal joint is long and exceedingly broad, almost triangular, with the expanded inner border overlapping the outer part of the mandibles and the lateral angle of the labrum, the produced anterior angle extends to the frontal plate and the second joint is inserted on the vertex of the triangle; the last named joint is short and slender, the third joint exceedingly small. The frontal plate is broadly triangular with obtuse vertex, completely occupying the small space between the foot of the antennulæ, the anterior angle of the antennæ, and the labrum. The labrum (*c*) scarcely of medium size, somewhat broader than the hemi-cylindrical hypopharynx. Hypopharynx, mandibles (*d*), maxillulæ, and maxillæ need no special mention. The left maxilliped is shown in Figure 2 *a*; the most interesting character is that the palp has almost disappeared, as we see but a somewhat produced angle. The border behind the maxillipeds is very well developed, with a number of small protuberances, and having on each side two oblique slender processes, of which the inner is long, the outer very long.

Thorax. Ovarian bosses are developed on all segments; they are very prominent, most of them almost semi-globular (on the drawn specimens they are accidentally — caused by pressure — more or less depressed on the right side of the second to the fourth segment); in the three anterior segments they are large and gradually decrease in size backward, the two posterior pairs almost petiolated, the seventh pair small (in the small specimen the two posterior pairs are even reduced to prominent, distally not swelled processes). The bosses do not occupy the sub-lateral part of the segments to its whole length, only the larger posterior portion, yet not extending to the posterior margin. The pleural plates are comparatively large, oblong, rounded, thus occupying the whole or at least most of the lateral margin; in the posterior segments they are broader and overlap each other considerably; their convex ventral side with numerous small tubercles and oblong knots. The three posterior segments on the ventral side with an interrupted row of very short fleshy keels; the other segments are not examined. The legs are robust; the second joint (Fig. 1 *b* and 1 *d*) on the outer side with a very high expansion, shaped as an oblique plate, which is about as high as long and somewhat shorter than the length of the joint, on both sides with irregular small protuberances; the other joints normal. In Figure 1 *b* is shown the first left leg with the marsupial plate; this plate shows on the under side a deep transverse furrow and more forward a group of low knots, on the upper side (Fig. 1 *c*) a kind of transverse keel, the marginal portion of which is divided into numerous irregular, small, thin-skinned processes. The basal part of the other four pairs of plates with numerous knots (Fig. 1 *a*). (The marsupium of both specimens with eggs.)

Abdomen. The five anterior segments with very large rounded pleural lamellæ, the anterior of which are somewhat transverse, the posterior oblong; the lamellæ cover the main part of one another, a large portion of the dorsal surface of the anterior segments, and the whole dorsal surface of the posterior ones. In Figure 1 the fifth pair of lamellæ are lettered a^5. The second to the fifth segments on the ventral side each with a transverse row of short fleshy processes or knots, or lamellar keels; the first segment with an interrupted series of low lamellæ. The sixth segment (posteriorly behind the attachment of the uropods produced into an oblong, distally rounded and swelled, almost petiolated process. Each pair of pleopods consists of two large rami; in the anterior pairs these are shorter and rather broadly triangular, backwards they gradually become elongate. The uropods biramous, the rami similar to those of the last pleopods; in Figure 1 *a* the visible distal part of the rami on the left side of the figure are marked with 6, on the right side with 6^1. The main part, or almost the whole, of both surfaces of the pleural lamellæ and of the pleopods and uropods is set with very low and irregular minute keels and more rounded protuberances, which are most developed on the anterior pleopods.

Size. The largest specimen — which has been taken as type for all the figures — is 14.2 mm. long to the end of the abdomen, 17.3 mm. long to the apex of the longest ramus of the uropods, and 10.9 mm. broad. The other specimen measures 15.6 mm. to the end of the uropods.

b. *Male.*

One specimen (Plate IV. Fig. 2 *b*) is symmetrical and undoubtedly normal; the other specimen (Fig. 2 *c*) is anomalous, not symmetrical, and somewhat misshapen, — especially the abdomen is conspicuously different. In the following the normal specimen is described, with some remarks concerning the other.

The body is considerably depressed and relatively broad, scarcely $2\frac{1}{2}$ times longer than broad.

Head. Its dorsal surface almost flat, with irregular rugosities. The eyes are very small and dark. The frontal part bends feebly downwards; the anterior margin is considerably curved. The antennulæ (Plate IV. Fig. 2 *d*) are rather long, 3-jointed; the basal joint thick, the second longer than the first and comparatively thick, the third rather short and slender. The antennæ of medium length, 3-jointed; the basal joint of medium length and almost twice as broad as long, with the outer margin concave; the second joint is attached to the anterior half of the outer margin of the first joint; it is stout and twice as long as the basal one; the third joint is rather short and slender. The labrum of medium size, with the anterior margin very convex; its median part is covered by the hypopharynx, which extends forward to the middle of the basal joint of the antennulæ. The hypopharynx is long, not broad, and tapers somewhat towards the rounded apex. The mandibles and the maxillulæ are easily seen in the figure; a rounded protuberance behind each maxillula most probably represents the maxilla; maxillipeds I have not been able to discover.

Thorax. The fifth segment is the broadest, and from that the thorax decreases a little in breadth towards both ends. The segments, when seen from above, with the lateral outline much rounded, but the incisions between them are short. On the ventral side a median, very conspicuous cone on each segment. The legs subequal in structure; all are relatively short and very thick, but the fourth and fifth pairs are somewhat larger and still more clumsy than the first pair; Figure 2 *e* (on Plate IV.) represents the left leg of the first pair, and a description is scarcely needed.

Abdomen. It does not occupy one third of the length of the body, and anteriorly it is somewhat narrower than the last thoracic segment; it is triangular with rounded angles, a little longer than broad, and the lateral outline is somewhat sinuous, which shape indicates the segmentation. All segments are completely fused; vestiges of transverse sutures are scarcely discernible on the dorsal, but rather distinct on the ventral side.

Size. The specimen is 3.3 mm. long.

The misshaped male is exhibited in Figure 2 *c* (on Plate IV.). The outline of the thorax is somewhat irregular; the abdomen is very wry, with all the segments well separated on the dorsal surface, and the last segment having about the shape of an oblique square. The result of this deformity is, in my opinion, very interesting.

Habitat. The label states that the two females (with their males) were found in the branchial cavity of *Munida refulgens* Fax., from Station 3378 (Lat. 3° 58′ 20″ N., Long. 81° 36′ W.), 112 fathoms.

12. **Pseudione galacanthæ**, n. sp.

Plate V. Fig. 2–2 *i*.

Five adult females and the same number of males have been transmitted. (Compare " Habitat.")

a. *Female.*

The body about 1½ times longer than broad.

Head. It is somewhat broader than long, fused with the considerably curved first thoracic segment and encircled forward to the antero-lateral angle, while its anterior margin is slightly curved; the frontal border is rather narrow and turned somewhat upwards; the dorsal surface is slightly convex. The antennulæ (Fig. 2 *b*, *a*) are in contact anteriorly, posteriorly they are separated by a small, triangular frontal plate (*p*); they are of about medium size, 3-jointed; the basal joint is rather large, thick, the second shorter and more slender, the third very small, terminating in an exceedingly short bristle. The antennæ (*b*) are 4-jointed, rather short; the basal joint is very large, forming almost an oblique oval, yet the inner margin is almost straight, the outer very convex, and the second joint originates from its extero-anterior angle; the second and third joints are short and slender, the fourth very small, terminating in an exceedingly short bristle. The frontal plate is already mentioned. The labrum is very broad; the hypopharynx is oblong-triangular with rounded vertex. Mandibles (*d*), maxillulæ (*e*), and maxillæ (*f*) do not present any interesting peculiarities. The left maxilliped is shown in Figure 2 *c*; the palp is very conspicuous, with some hairs, but not jointed. The border behind the maxillipeds is well developed, with numerous small, irregular protuberances, and only one pair of processes which are long and distally narrow.

Thorax. The four anterior segments with ovarian bosses, which are low, and occupy about two thirds of the lateral margin of each segment; the pleural plates which occupy the remaining one third of the margin, are short or narrow. The three posterior segments without bosses, but the pleural plates occupy the entire margin and are developed as lamellæ, increasing gradually in length and turning more backward from the fifth to the seventh segment; besides they are longer on the convex than on the other side of the animal. The legs are rather stout (Fig. 2 *d* and Fig. 2 *e*); the second joint about as broad as long, owing to the fact that on the whole outer side it is much expanded, with the outline almost semicircular; the fourth joint with a keel on the inner margin, and two short, knot-like keels are found on the same margin of the posterior, but disappear on the anterior pairs of legs. The first left leg, with its marsupial plate, is shown in Fig. 2 *d*; the plate has on the lower side a broad and high transverse keel, and on the upper side a structure similar to that in Munidion (see above). Only the last segment on the ventral side with numerous small incisions and between these low fleshy projections; this structure is found both at the anterior and the posterior margin of the segment.

Abdomen. It occupies less than one third of the length of the animal, and the segments are well separated on the dorsal surface. The pleural plates are very large and lamellar, partly overlapping one another, in the first segment somewhat longer than those of the last thoracic segment, and then gradually increasing in length and turning more backward from the first to the fifth segment. The ventral side of the five anterior segments about as in the preceding species. Each pleopod with two triangular or ovate rami of medium size ; the pleopods decrease somewhat in size from before backward, and the outer ramus is as a rule a little smaller than the inner one. Each uropod consists of one ramus (Fig. 2 *b*) which is oblong-ovate and considerably smaller than the pleural plates of the fifth abdominal segment.

Size. The largest specimen is 10.4 mm. long to the apex of the sixth abdominal segment, 11.8 mm. to the end of the uropods, and 7.4 mm. broad. The smallest specimen — with eggs in the marsupium — is only 7 mm. long to the end of the abdomen, and 5.8 mm. broad.

b. *Male.*

The body is very elongate (Fig. 2 *f*), between 3½ and 4 times longer than broad.

Head. The dorsal surface is convex, the antero-lateral margin much curved, and the anterior part of the head bends somewhat downward. Eyes could not be detected, but we find small frontal impressions, which vary very much in different specimens (in one specimen two pairs were found). The antennulæ (Fig. 2 *g*) of medium length, 3-jointed ; the basal joint thick and almost globular, the second shorter and much narrower than the first, the third minute. The antennæ of medium length, 5-jointed ; the first joint thick and almost globular ; the three following joints gradually a little shorter and much narrower; the apical joint minute. The labrum extremely broad, crescent-shaped. The hypopharynx reaches to the middle of the labrum ; it is rather long, of medium breadth, tapering somewhat towards the rounded end. Mandibles, maxillulæ, and maxillæ (*f*) normal ; the maxilliped (*g*) has the shape of a rather small oblong triangle.

Thorax. The fifth segment is the broadest, a little broader than the seventh, and considerably broader than the first segment. The lateral outline of the segments either rounded or (Fig. 2 *f*) more straight with rounded angles ; the incisions between the segments narrow, triangular, and very deep. The ventral surface without conical protuberances. The legs more slender than in the preceding form ; from before backward to the fifth pair they increase a little in length and their hand in size, and from the fifth to the last pair at least the hand decreases somewhat in size. In Figure 2 *h* is shown the left leg of the first pair, and in Figure 2 *i* that of the seventh pair.

Abdomen. It occupies about two fifths of the total length of the animal, and decreases in breadth from before backward to the small square sixth segment. All segments are very movable ; seen from above, their lateral portion in the large specimen is triangular with the lateral angles more or less acute, in the small specimens less triangular and rounded laterally. In the anterior segments rudiments of pleopods are either scarcely discernible or visible as very low and broad rounded eminences.

Size. The largest specimen (Fig. 2 *f*) is 4.8 mm. long; a smaller specimen from which the three analytical figures have been drawn, is 3.5 mm. long; a small specimen is only 2.9 mm. long.

Habitat. The label indicates that the five adult females (with their males) were found in the branchial cavity of *Galacantha diomedeæ* var. *parvispina* Fax., from Station 3435 (Lat. 26° 48′ 0″ N., Long. 110° 45′ 20″ W.), 859 fathoms. In the Report on the Stalk-eyed Crustacea of the "Albatross" Expedition of 1891, W. Faxon writes (p. 81): "Seven specimens (5 males, 2 females) of var. *parvispina* house a Bopyrus in the left branchial chamber."

13. **Parargeia ornata,** n. gen., n. sp.

Plate VI. Fig. 1–1 *i*.

Only one female and its male are found.

a. *Female.*

The body is much distorted and scarcely 1⅛ times longer than broad.

Head. It is comparatively very broad, but otherwise of the same shape as in *Munidion* (*ante*, p. 115). The antennulæ (Fig. 1 *b*) separated by a frontal plate (*p*), of medium size, 3-jointed; the basal joint comparatively long and thick, the second short and narrow, the third exceedingly small. The antennæ (*b*) similar in shape to those of Pseudione (see above), but larger and 6-jointed; the basal joint very large, forming about an oblong oval, with both margins a little convex; the second joint is attached at the antero-exterior angle of the first, and is tolerably short and slender, yet longer and considerably thicker than the third; the three distal joints are exceedingly small. The frontal plate (*p*) rather large, about three times broader than long, anteriorly emarginate. The labrum exceedingly large, in the middle very short, but on each side forming a large oblique plate (*c*) which overlaps the distal part of the mandible and the maxillula, and the lateral part of the hypopharynx. This organ (*h*) is triangular and broader towards its base than in the preceding forms. The mandibles (*d*) extend in the middle with their acute tip beyond the end of the hypopharynx. Maxillulæ (*e*) and maxillæ (*f*) need no mention. The left maxilliped is shown in Figure 1 *c*; the palp consists of a prominent basal part and a small terminal joint. The border behind the maxillipeds well developed, with two pairs of long, oblique, distally slender processes.

Thorax. Ovarian bosses are found on the four anterior segments; they are oblong, considerably convex, and occupy from less to more than half of the sub-lateral portion of each segment. By a conspicuous or even deep furrow they are set off from the anterior part of the pleural plates, which lie outside or more beneath the bosses, are much arched, and look almost like "epimera" in

Cymothoidæ. The posterior portion of the lateral part of the segments mentioned is more or less protruding, rounded or angular, and must be considered as the posterior division of the pleural plate (compare *Cryptione*). On the three posterior segments the pleural plates are deeply incised, divided into a larger, broader, and more produced anterior part, and a much smaller, narrower, and less produced posterior one, which is more or less obsolete on the last segment. At least on the posterior segments the ventral side shows the usual low fleshy keels. The legs are slender; the second joint proximally on the outer side with a considerable rounded expansion, which is comparatively longer and broader on the anterior (Fig. 1 *d*) than on the posterior (Fig. 1 *e*) pairs; the other joints are normal. In Figure 1 *d* is shown the first leg with its unusually large marsupial plate; the transverse furrow is not deep; on the upper side the keel is tolerably high and much compressed, but without marginal processes. The marsupial plates do not quite reach each other at the middle; their natural position was somewhat disturbed in the specimen, and therefore it was necessary to make use of construction in Figure 1 *a*.

Abdomen. The segments distinctly separated at the middle on the flat dorsal surface. No pleural plates. The segments fleshy on the ventral side; only the first segment with slight furrows. The pleopods very curious, and rather similar to each other; each consists of two rami; the outer ramus is a very long, subrectangular or distally rounded, somewhat fleshy lamella, which is placed at the margin of the segment; the inner ramus is proportionally short, more or less ovate, fleshy, originating at some distance from the outer ramus, and on the left side of the animal it conveys the impression that the basal half is fused with the ventral side of the segment. (I am aware that another interpretation of the described facts could be advanced, namely, that the outer ramus is a pleural plate set off by a kind of articulation, and that the inner ramus in reality represents the entire pleopod, but this opinion I cannot share.) Each uropod consists of a single lamella of about the same shape and size as the nearest outer ramus of a pleopod.

Size. The specimen is 8.5 mm. long to the apex of the abdomen, 10.3 mm. long to the end of the uropods, and 7.2 mm. broad.

b. *Male.*

The shape of the body is interesting. It increases uniformly but rather slightly in breadth from the head to the last thoracic segment, and the abdomen is anteriorly somewhat broader than the preceding segment, triangular with rounded angles, somewhat broader than long, the anterior margin a little concave and the lateral margins convex. The body is a little more than 2½ times longer than the width of the abdomen.

Head. The dorsal surface is convex, the median part of the anterior outline almost straight. A pair of small spots or minute depressions perhaps represent the eyes. When the head is seen from below (Fig. 1 *g*), it is observed that the frontal border arises like a broad and rather high transverse keel above the attachment of antennulæ and antennæ. The antennulæ of medium length, 3-jointed; the basal joint thick, the second shorter and much narrower than the first, the third short and very slender. The antennæ rather short, 7-jointed; the first joint very thick, the second of about the same length but somewhat more slender, the third somewhat shorter and more slender than the second, the fourth rather short and very slender; the three distal joints exceedingly small. The mouth forms a basally broad, somewhat protruding oblique cone, but without a dissection I was not able to recognize several of the parts with any certainty; the figure will show what I believed I saw.

Thorax. The segments much arched on the dorsal side, the incisions between them of medium length, and most of them very narrow; their lateral margin is, when seen from the side, much more rounded than if seen from above. No ventral cones. The legs increase somewhat in length from before backward, but at the same time their hand decreases in size from the first (Fig. 1 *h*) to the seventh (Fig. 1 *i*) pair, and besides alters conspicuously in shape.

Abdomen. It occupies somewhat more than one fourth of the length of the animal; its outline is described above. All segments are completely fused, so that only some transverse, partly very indistinct furrows, but no sutures, are found on the dorsal surface. About half way between the median line and the lateral margin the dorsal surface presents a broad longitudinal depression, and in the median line a little behind the anterior margin a prominent knot. The ventral surface does not seem to be quite normal, but the following characters certainly are of importance: no rudiments of pleopods are to be discovered, but in the median line are found three protuberances: the first small, the second rather large, the third shaped as a short transverse keel.

Size. The specimen is 4.1 mm. long.

Habitat. In the branchial cavity of *Sclerocrangon procax* Fax., from Station 3418 (Lat. 16° 33′ N., Long. 99° 52′ 30″ W.), 660 fathoms, 1 female with a male.

14. Bathygyge grandis, n. gen., n. sp.

Plate VI. Fig. 2–2 *c*.

Only a male, and the posterior part of a female have been sent to me.

a. *Female.*

The rudiment consists of the posterior part of the thorax, bearing three legs on one and two on the other side, and the abdomen.

Thorax. The pleural plates are very large oval lamellæ, only connected with the segment by somewhat less than the posterior half of their interior margin, and this result is due to the fact that they anteriorly are very much produced, highly overlapping each other, and posteriorly rather shortly produced. The legs are tolerably slender; the second joint not expanded; the fifth joint elongate, in the last pair as long as the hand.

Abdomen. It is turned to the left in a startling degree, and is proportionally small, — perhaps very small. The dorsal surface is soft-skinned, the segments more or less distinctly separated. Pleural plates not developed. The pleopods quite soft, of medium size, decreasing conspicuously in size from before backward and attached to the lateral margin; each pleopod consists of a short peduncle and two lamellar oblong rami; the outer ramus much larger than the inner one. The uropods biramous; the outer ramus a little smaller than the outer of the fifth pleopod, the inner ramus very short, almost rudimentary. The pleopods are curled to such a degree that it would have been impossible without much construction to draw a sketch of the abdomen.

b. *Male.*

The body is a little more than three times longer than broad, and from the fourth thoracic segment it decreases in breadth towards both ends (Fig. 2).

Head. The dorsal surface rather convex; the median portion of the anterior margin almost straight. No eyes. The frontal border bent slightly downwards (Fig. 2 *a*). The antennulæ rather short, 3-jointed; the basal joint tolerably thick, and partly overlapped by the rostrum; the second joint slender and rather short, the third very small. The antennæ comparatively long, 7-jointed; the four proximal joints of about the same length, but decreasing much in breadth from the rather thick basal joint to the fourth one; the fifth joint is short and very slender, the two last joints exceedingly small. The mouth forms a rostrum which, when seen from below, is triangular, considerably depressed and directed forward, reaching almost to the frontal margin of the head. The hypopharynx is very large, and just outside it is seen the very oblong lateral part of the labrum (*d*), the median part of which is concealed by the hypopharynx; at first I believed that these oblong organs were the mandibles, but a closer examination gave the result mentioned, while the mandibles, being needles with brown apex, were discovered within the rostrum. Maxillulæ are not observed; the maxillæ (*f*) are small semicircular lobes lying considerably behind the posterior edge of the labrum. The maxillipeds (*g*) are short, extremely slender, almost styliform.

Thorax. The segments are rather convex, the incisions between them comparatively broad and very deep; the lateral margins are much curved when seen from the side. The legs increase considerably in length, and very much in thickness, from the first (Fig. 2 *b*) to the fifth pair (Fig. 2 *c*) which is robust, with the hand very large; the two posterior pairs again decrease somewhat in size. The terminal margin of the hand is deeply concave, thus differing considerably from the preceding forms.

Abdomen. It occupies scarcely one fourth of the length of the animal; it is narrower than the last thoracic segment, shortly ovate in outline, without the slightest rudiment of segmentation or abdominal feet; both the ventral and especially the dorsal surface are very convex.

Size. Uncommonly large, being 7 mm. long, and 2.3 mm. broad.

Habitat. The branchial cavity of *Glyphocrangon spinulosa* Fax., from Station 3424 (Lat. 21° 15′ N., Long. 106° 23′ W.), 676 fathoms, 1 female with its male.

Remarks. The species is established essentially on the very large male, the mouth parts of which are very different from those of other forms known to me. I hope that it will prove to be rather easy to recognize the form, but I hesitated to establish the new genus, the knowledge of the female being very incomplete. However, I found it impossible to refer the species to any of the genera hitherto published.

ONISCIDÆ.

15. Porcellio lævis Latr. (1804).

I will only refer to the account in G. Budde-Lund's Crustacea Isopoda Terrestria, 1885, which is the principal work on the Oniscidæ; the author (pp. 138–140) describes the species, presents an enormous quantity of synonymy and references to earlier authors, and adds a very long list of localities for this almost cosmopolitan form.

Habitat. Chatham Island, Galapagos (March 29, 1891), four specimens (determined by G. Budde-Lund).

Zoölogical Museum, Copenhagen,
September 16, 1897.

EXPLANATION OF THE PLATES.

PLATE I.

1. *Eurycope pulchra*, n. sp.

Fig. 1. Female seen from above, × $\frac{9}{4}$. Of the antennulæ only the two proximal joints, of the antennæ only the four proximal joints are drawn; the thoracic legs omitted, with the exception of the basal joint of the four anterior pairs.

Fig. 1 *a*. Female seen from left side, × $\frac{9}{4}$. Antennulæ and antennæ as in the preceding figure; the first thoracic leg is drawn, but of the six other pairs only the basal and the major part of the second joint are shown.

Fig. 1 *b*. Right mandible seen from below, × 11.

Fig. 1 *c*. Left mandible seen from below, × 11; most of the palp omitted; *a*, cutting portion; *b*, molar process; *l*, lacinia mobilis; *m*, muscle (only the basal part); *p*, palp (proximal part).

Fig. 1 *d*. Left maxillula seen from below, × 11; 1, first joint; l^1, lobe of the first joint; 2, second joint; 3, third joint; l^3, lobe of the third joint.

Fig. 1 *e*. Left maxilla seen from below, × 11; 1, first joint; 2, second joint; l^2 lobe of the second joint; 3, third joint; l^3, lobes of the third joint.

Fig. 1 *f*. Left maxilliped seen from below, × 11; 1, first joint, *ep.* its epipod; 2, second joint; *h*, its coupling hooks; l^2, lobe of the second joint; 7, seventh joint.

Fig. 1 *g*. First thoracic leg, × $\frac{9}{2}$.

Fig. 1 *h*. Thoracic leg of fifth pair, × $\frac{9}{2}$; the natatory hairs omitted; 1, first joint; 2, second joint; 7, seventh joint. This and the preceding analytical figures are drawn from parts of a female.

Fig. 1 *i*. Abdomen of a male seen from below, × $\frac{11}{3}$; *a*, pleopod of first pair; *b*, pleopod of second pair; *c*, uropod; *d*, anal doors.

2. *Eurycope scabra*, n. sp.

Fig. 2. Female seen from above, × 2. The antennulæ completely wanting; of the antennæ the four proximal joints, and of the thoracic legs only the basal joint are seen. As to the correctness of the outline of thorax and abdomen, see the description.

Fig. 2 *a*. Left mandible seen from below, × $\frac{25}{2}$.

Fig. 2 *b*. Left maxillula seen from below, × $\frac{25}{2}$.

Fig. 2 *c*. Left maxilla seen from below, × $\frac{25}{2}$.

Fig. 2 *d*. Left maxilliped seen from below, × $\frac{25}{2}$.

PLATE II.

1. *Eurycope scabra*, n. sp. (continued).

Fig. 1. First thoracic leg of female seen from the exterior side, × 6.

2. *Æga maxima*, n. sp.

Fig. 2. Female without marsupium, natural size; the apex of the last abdominal segment was wanting.

Fig. 2 *a*. Right side of thorax of the same specimen showing the "epimera," etc., natural size.

Fig. 2 *b*. Left leg of the second pair of the same specimen seen from below, scarcely × 3.

Fig. 2 *c*. Left leg of the fifth pair seen from below, scarcely × 3.

3. *Æga acuminata*, n. sp.

Fig. 3. Head of female without marsupium, seen half from above and half from in front, × 3.

Fig. 3 *a*. Right side of thorax and of the two anterior abdominal segments of the same specimen, × 2.

Fig. 3 *b*. Posterior part of abdomen with the uropods of the same specimen, scarcely × 3.

4. *Æga plebeia*, n. sp.

Fig. 4. Head and first thoracic segment of a good-sized female without marsupium, seen half from above and half from in front, × $\frac{8}{3}$.

Fig. 4 *a*. Right side of thorax and of the two anterior abdominal segments of the same specimen, × $\frac{7}{3}$.

Fig. 4 *b*. Left leg of second pair of the same specimen, seen from below, × $\frac{9}{2}$.

Fig. 4 *c*. Left leg of fifth pair of the same specimen, seen from below, × $\frac{9}{2}$.

Fig. 4 *d*. Posterior part of the abdomen with the uropods of the same specimen, × $\frac{8}{3}$. The hairs and spines on the uropods and on the posterior margin of the last abdominal segment omitted.

5. *Æga longicornis*, n. sp.

Fig. 5. Female without marsupium, × about $\frac{8}{3}$.

Fig. 5 *a*. Right side of thorax and of the two anterior abdominal segments of the same specimen, × $\frac{9}{2}$.

Fig. 5 *b*. Posterior part of abdomen with the uropods of the same specimen, × $\frac{11}{2}$.

PLATE III.

1. *Æga longicornis*, n. sp. (continued).

Fig. 1. Left leg of second pair of the female exhibited in the preceding plate, seen from below, × $\frac{13}{2}$.

Fig. 1 *a*. Left leg of fifth pair of the same female, seen from below, × $\frac{13}{2}$.

2. *Rocinela laticauda*, n. sp.

Fig. 2. Male (the largest specimen), natural size.

Fig. 2 *a*. Head of female without marsupium, seen from below, × 5.

Fig. 2 *b*. Right side of thorax of the small immature female, scarcely × 3.

Fig. 2 *c*. Left leg of second pair of the larger immature female, seen from below, scarcely × 4.

Fig. 2 *d*. Left leg of fifth pair of the same female, seen from below, scarcely × 4.

Fig. 2 *e*. Last thoracic segment and abdomen of the small immature female, scarcely × 3.

3. *Rocinela modesta*, n. sp.

Fig. 3. Head of female with marsupium, seen from below, × 6; the flagella of the antennæ are broken off.

Fig. 3 *a*. Left leg of second pair of the same female, seen from below, × $\frac{19}{3}$.

Fig. 3 *b*. Left leg of fifth pair of the same female, seen from below, × $\frac{19}{3}$.

Fig. 3 *c*. Last thoracic segment and abdomen of the same female, × 3.

4. *Irona foveolata*, n. sp.

Fig. 4. Female with marsupium, × $\frac{7}{3}$.

Fig. 4 *a*. Leg of second pair of "pullus stadii primi," × 22.

Fig. 4 *b*. Posterior part of abdomen of "pullus stadii primi," × 22.

5. *Cryptione elongata*, n. gen., n. sp.

Fig. 5. Leg of first pair of the male, × 111.

Fig. 5 *a*. Leg of fifth pair of the male, × 111.

PLATE IV.

1. *Cryptione elongata*, n. gen., n. sp. (continued).

Fig. 1. Female seen from above, × $\frac{13}{3}$.

Fig. 1 *a*. Same female seen from below, × $\frac{13}{3}$; *m*. male; *mxp*. maxilliped; 1′, rami of first pleopod on the left side (of the animal = right side of the figure); 2, rami of second pleopod on the right side; 4′, rami of fourth pleopod on the left side; 5, rami of fifth pleopod on the right side; 5′, rami of fifth pleopod on the left side; 6, uropods. The marginal hairs on the marsupial plates are omitted.

Fig. 1 *b*. Head of the female seen from below and both maxillipeds omitted, × 9; *a*, antennula; *b*, antenna; *c*, labrum; *d*, mandible; *e*, maxillula; *f*, maxilla; *g*, place of attachment of the maxilliped; *h*, hypopharynx; *l*, lobes or processes from the border behind the maxillipeds.

Fig. 1 *c*. Left maxilliped of the same female seen from below, × $\frac{19}{2}$; 1, first joint with its posterior expansion; 2, second joint; d^2, dilatation on the outer side of the second joint; *p*, palp.

Fig. 1 *d*. Left leg of first pair with its marsupial plate seen from below, × $\frac{19}{2}$; 2, second joint of the leg (the first joint being fused with the thorax).

Fig. 1 *e*. Male seen from above, × $\frac{19}{2}$.
Fig. 1 *f*. Same male seen from below, × $\frac{25}{2}$.
Fig. 1 *g*. Head of the same male seen from below, × 36.

2. *Munidion princeps*, n. gen., n. sp.

Fig. 2. Anterior part of the head of the large female seen from below, scarcely × 10; *c*, labrum; *d*, mandible; *f*, maxilla.
Fig. 2 *a*. Left maxilliped of the large female, seen from below, scarcely × 7.
Fig. 2 *b*. Normal male, × $\frac{23}{2}$.
Fig. 2 *c*. Misshaped male, × $\frac{23}{2}$.
Fig. 2 *d*. Head of the normal male, seen from below, × 39.
Fig. 2 *e*. Left leg of first pair of the normal male, × 44.

PLATE V.

1. *Munidion princeps*, n. gen., n. sp. (continued).

Fig. 1. The large female seen from above, about × $\frac{16}{5}$; a^5, pleural plates of the fifth abdominal segment.
Fig. 1 *a*. Same female seen from below, about × $\frac{16}{5}$; 1, rami of first pleopod on the right side (of the animal, left side of the figure); 1′, rami of first pleopod on the left side; 4, rami of fourth pleopod on the right side; 5, rami of fifth pleopod on the right side; 5′, rami of fifth pleopod on the left side; 6, rami of the right uropod; 6′, rami of the left uropod.
Fig. 1 *b*. Left leg of first pair with its marsupial plate of the same female, seen from below, scarcely × 7.
Fig. 1 *c*. Posterior part of the marsupial plate exhibited in the preceding figure, and seen from above, × $\frac{19}{2}$.
Fig. 1 *d*. Left leg of sixth pair of the same female, scarcely × 7.

2. *Pseudione galacanthæ*, n. sp.

Fig. 2. Large female, seen from above, × $\frac{9}{2}$; 6, uropods.
Fig. 2 *a*. Same female seen from below, × $\frac{9}{2}$; 1′, rami of first pleopod on the left side (of the animal); 4′, rami of fourth pleopod on the left side; 5, rami of fifth pleopod on the right side; 5′, rami of fifth pleopod on the left side; a^5, pleural plates of fifth abdominal segment.
Fig. 2 *b*. Anterior part of the head of female, seen from below, × 10; *a*, antennula; *b*, antenna; *c*, labrum; *d*, mandible; *e*, maxillula; *f*, maxilla; *p*, frontal plate.
Fig. 2 *c*. Left maxilliped of female, seen from below, × 10.
Fig. 2 *d*. Left leg of first pair with its marsupial plate, seen from below, × 10.
Fig. 2 *e*. Left leg of sixth pair of female, × 10.
Fig. 2 *f*. Largest male, × 10.
Fig. 2 *g*. Head and a part of the first thoracic segment of a smaller male seen from below, × 39; *f*, maxilla; *g*, maxilliped.
Fig. 2 *h*. Left leg of first pair of the last named male, × 47.
Fig. 2 *i*. Left leg of seventh pair of the same male, × 47.

PLATE VI.

1. *Parargeia ornata*, n. gen., n. sp.

Fig. 1. Female seen from above, about × $\frac{9}{2}$.
Fig. 1 *a*. Same female seen from below, about × $\frac{9}{2}$; as to the marsupial plates see the description of the species.
Fig. 1 *b*. Anterior part of the head of the same female seen from below, × 13; *b*, antenna; *c*, labrum; *d*, mandible; *e*, maxillula; *f*, maxilla; *h*, hypopharynx; *p*, frontal plate.
Fig. 1 *c*. Left maxilliped of the same female seen from below, scarcely × 10.
Fig. 1 *d*. Left leg of first pair with its marsupial plate seen from below, scarcely × 10.
Fig. 1 *e*. Left leg of seventh pair of the same female, scarcely × 10.
Fig. 1 *f*. Male, × $\frac{29}{3}$.
Fig. 1 *g*. Head of the same male seen from below, × 39.
Fig. 1 *h*. Left leg of first pair of the same male, × 46.
Fig. 1 *i*. Left leg of seventh pair of the same male, × 46.

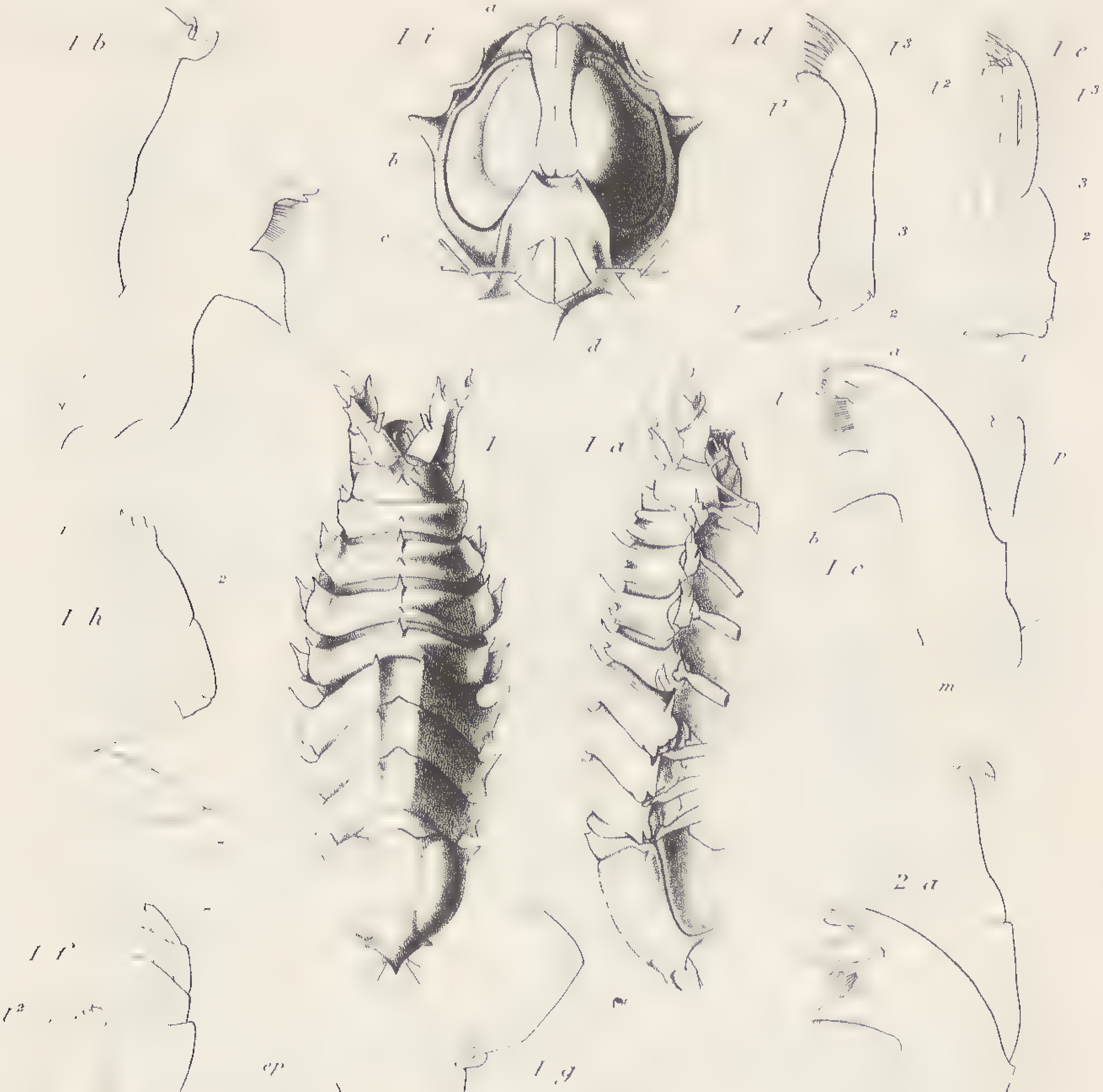
2. *Bathygyge grandis*, n. sp.

Fig. 2. Male, scarcely × $\frac{13}{2}$.
Fig. 2 *a*. Head of the male seen from below, × 26; *d* (by error instead of *c*), labrum; *f*, maxilla; *g*, maxilliped.
Fig. 2 *b*. Left leg of first pair of the male, × 19.
Fig. 2 *c*. Left leg of fifth pair of the male, × 19.

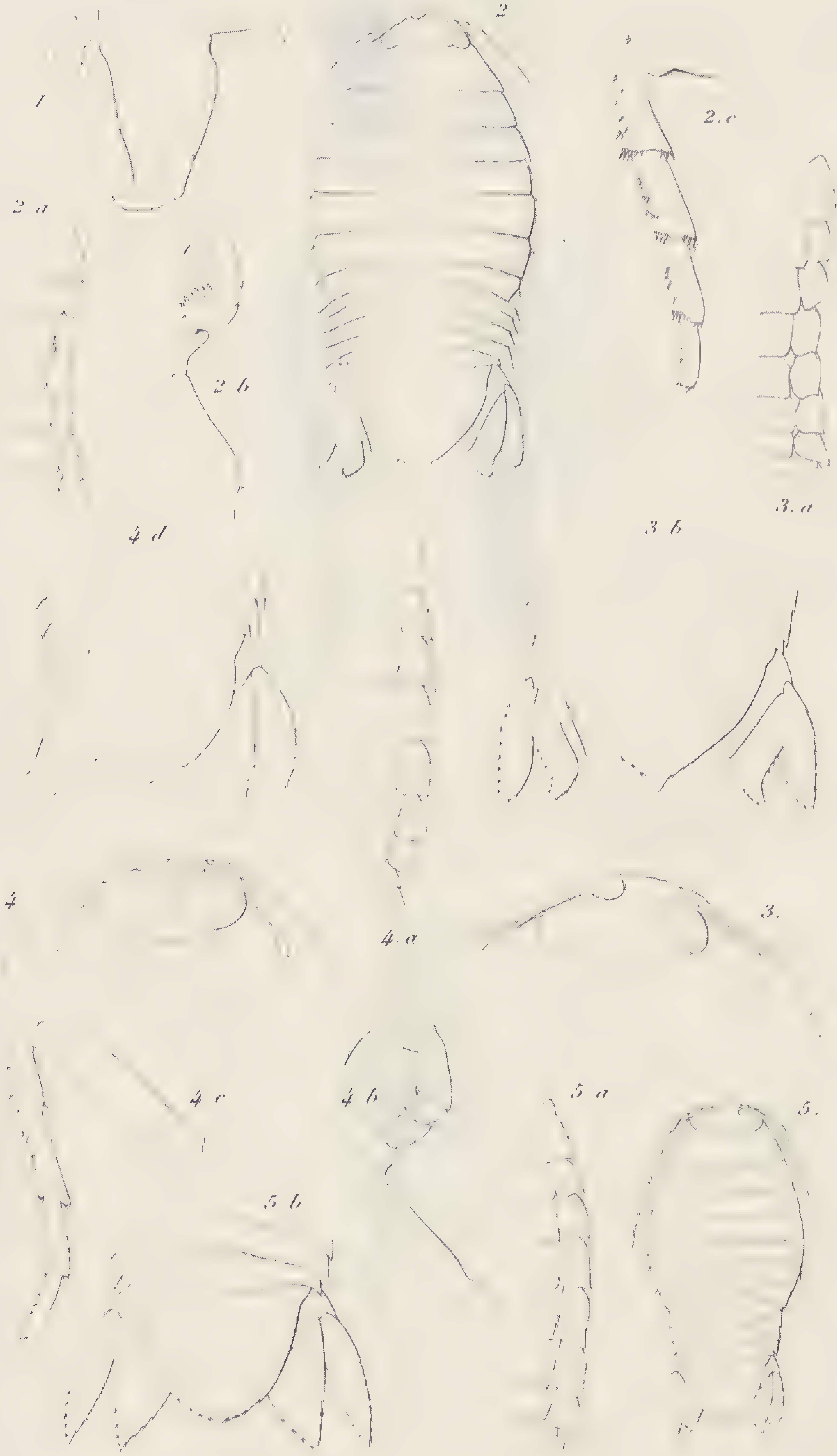
PLATE VII.

ROUTE OF THE "ALBATROSS."

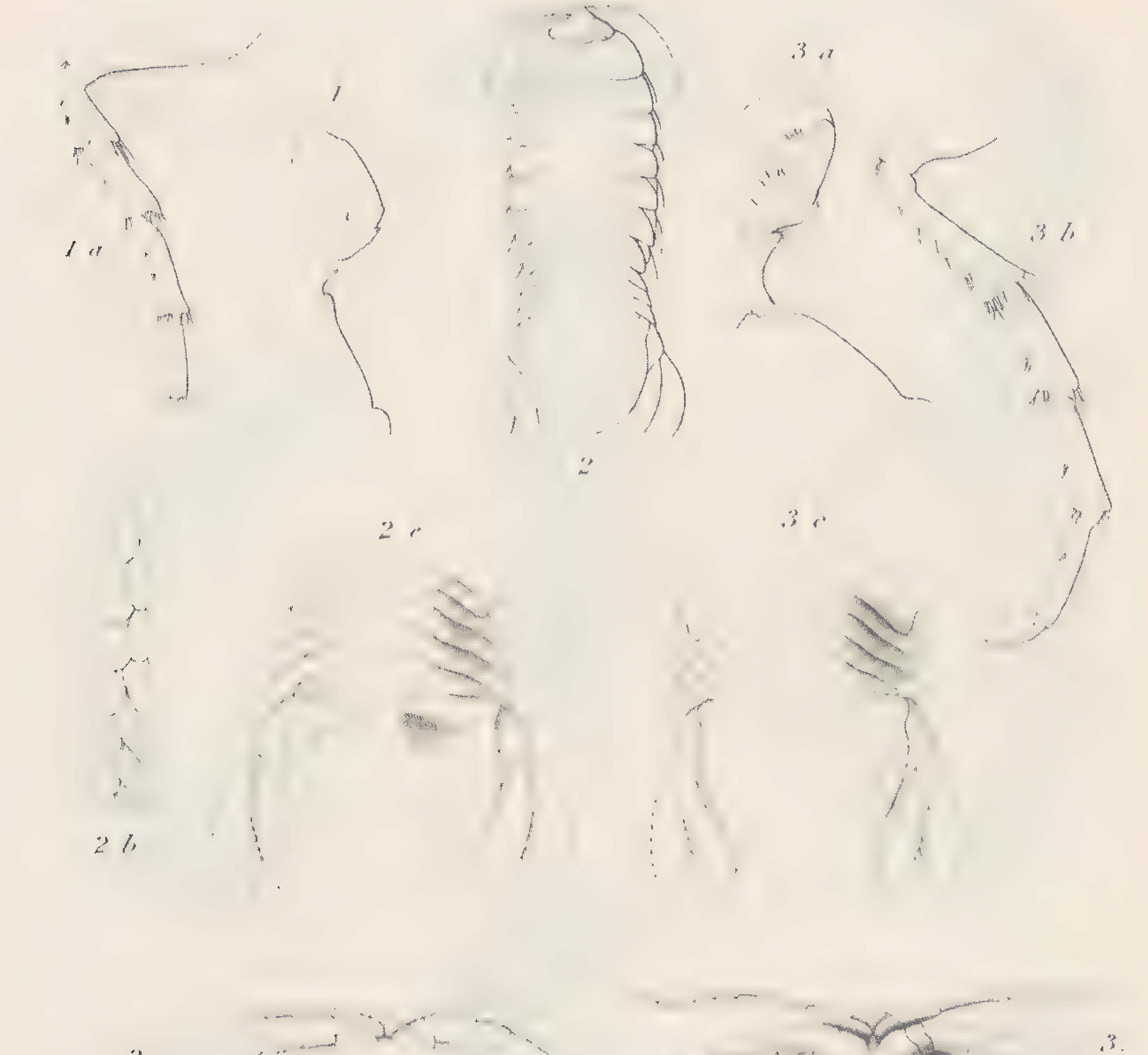
EXPLORATIONS OF THE
U.S. FISH COMMISSION
STEAMER ALBATROSS
Lieut. Comdr. Z.L. Tanner. U.S.N., Comdg.
February to April 1891
Compiled from the latest U.S. Hydrographic Office charts with additions by the U.S.F.C. Steamer Albatross
Soundings represented thus 2256 are by the U.S.F.C. Str. "Albatross" 1888
" " 2280 " " " 1889
" " 2232 " " " 1891
" " 2004 are from other sources
100 fathom line shown thus
500 "
1000 "
1500 "
2000 "
P Pebbles, Co coral, Gl globigerina, M mud, O ooze, S sand, Sh shells, Sp specks, G gravel, fne fine, hrd hard, sft soft, rky rocky, brk broken, bk black, rd red, gn green, gy gray, yl yellow, bn brown, dk dark, lt light, wh white
MEXICO
GUATEMALA
HONDURAS
SALVADOR
NICARAGUA
COSTA RICA
COLOMBIA
GULF OF MEXICO
CARIBBEAN SEA
Gulf of Panama
GALAPAGOS ISLANDS
REVILLA GIGEDO ISLANDS
GUAYMAS
Agiabampo
Topolobampo
Altata
MAZATLAN
San Blas
Banderas Bay
C. CORRIENTES
Manzanillo
Maruata
Petacalco Bay
ACAPULCO
P. Angeles
Salina Cruz
TEHUANTEPEC
La Puerta
Champerico
S. Jose
Acajutla
La Libertad
Gulf of Fonseca
Corinto
Gulf of Nicoya
Gulf of Dulce
C. Mala
Mariato Pt.
PANAMA
Chiriqui
Chocó Bay
Gorgona
C. SAN FRANCISCO
C. San Lorenzo
Malpelo I.
Cocos I.
Tower I.
Culpepper I.
Wenman I.
Abingdon I.
Albemarle I.
Indefatigable I.
Chatham I.
Charles I.
Hood I.
Narborough I.
Clarion
Socorro
San Benedicto
Roca Partida
C. SAN LUCAS
LA PAZ
Magdalena Bay
C. SAN LAZARO
Concepcion Bay
Carmen
CALIFORNIA
Tres Marias
Track of the U.S.F.C. Str. "Albatross" 1891
500 fathoms
1000 fathoms
1500 fathoms
2000 fathoms
105°
100°
95°
90°
85°
80°
75°
110°
115°
30°
25°
20°
15°
10°
5°
0°


1 b
1 i
1 d
1 e
a
b
c
d
l^1
l^2
l^3
1
2
3
1
1 a
1 c
p
m
1 h
2 a
1 f
l^2
h
ep
1 g
2
2.
2 b
2 c
2 d

H. J. Hansen del. Lovendal sc.

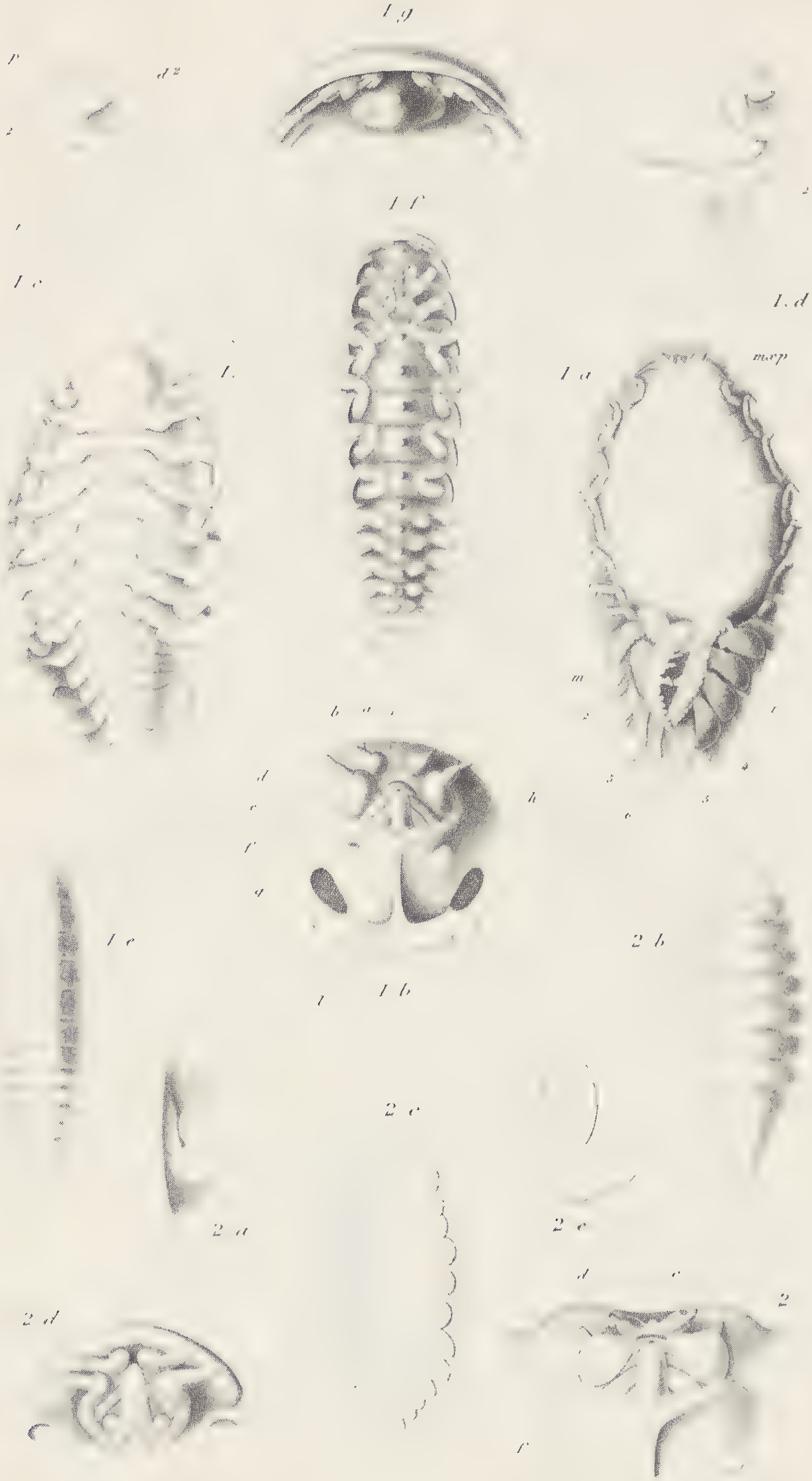

1
2
2. c
2. a
2. b
3. a
3. b
4. d
4
4. a
3.
4. c
4. b
5. a
5.
5. b

H. J. Hansen del. Lövendal sc.

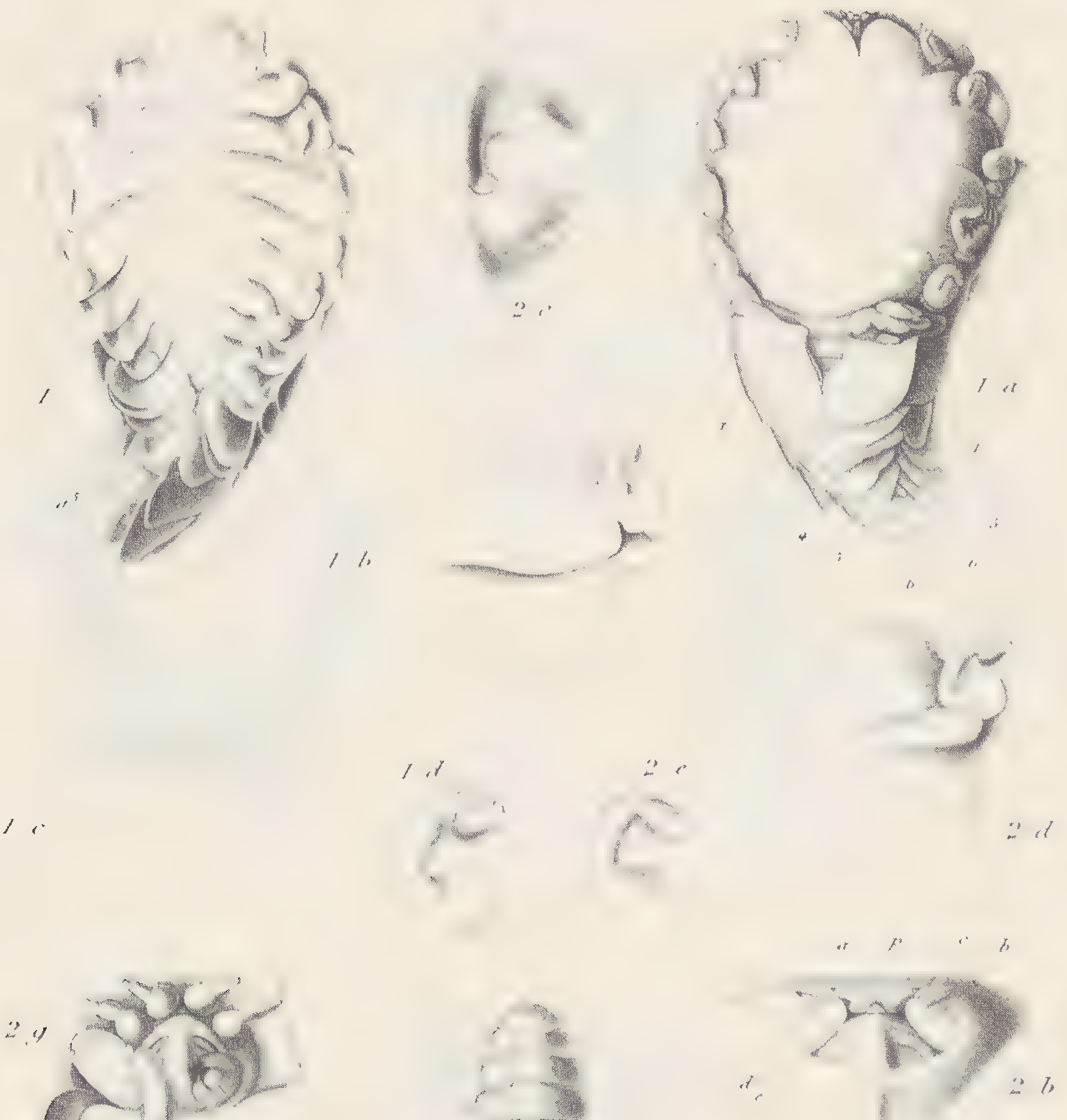

1 a
1
2
3 a
3 b
2 e
3 c
2 b
2 a
3.
2 c
4 a
4
4 b
2 d
5 a
5

H. J. Hansen del.

Lövendal sc.

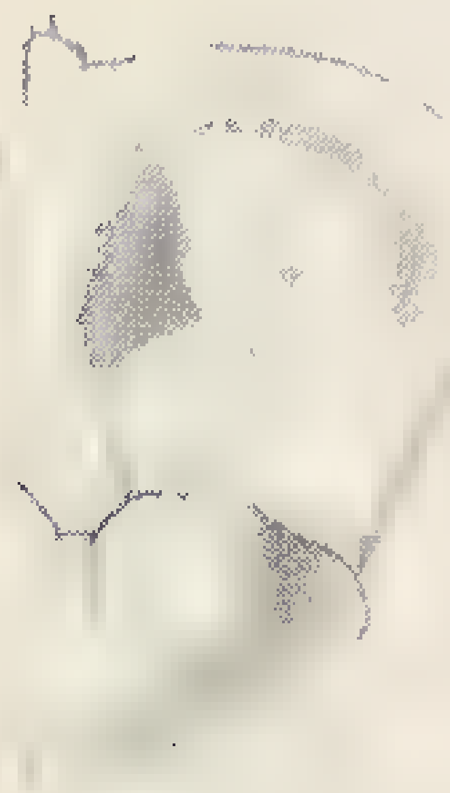

1 g
p
d²
1 f
1 c
1 d
msp
1 a
1
m
b a c
d
e
f
g
h
1 e
2 b
1 b
2 c
2 a
2 e
2 d
d
e
2
f

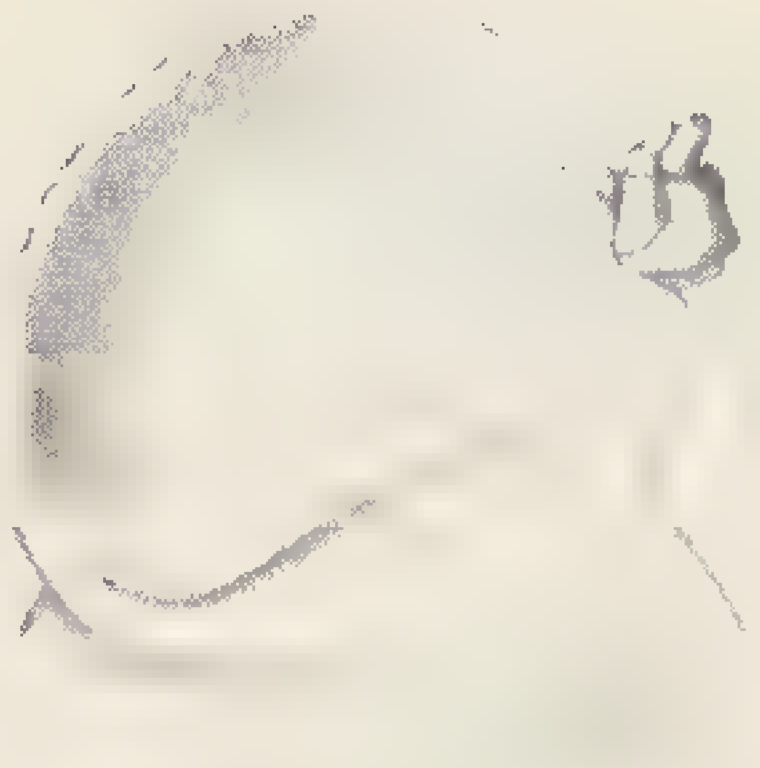
H. J. Hansen del. Lovendal sc.

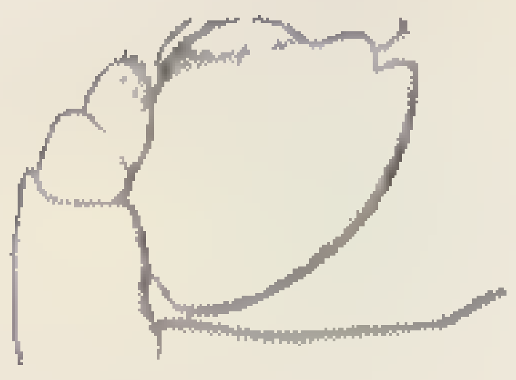

1
a⁵
2 e
1 a
r
1
5
4
3
6
6
1 b
1 d
2 c
1 c
2 d
a
P
c
b
2 g
a
r
d
c
r
2 b
2 f
2
2 a
2 h
2 i
r
6
5
a⁵
5
4

H J Hansen del

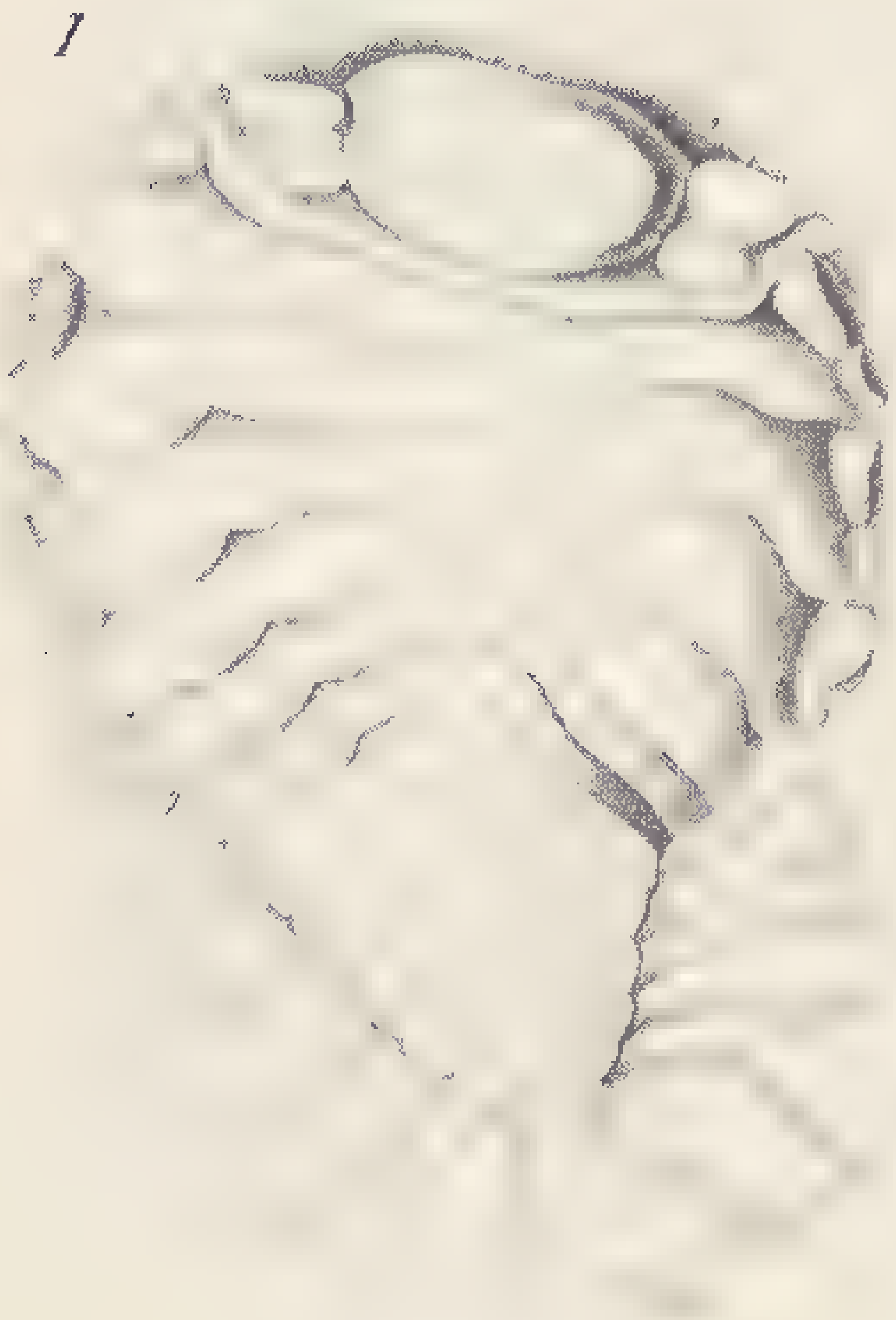
Lövendal sc

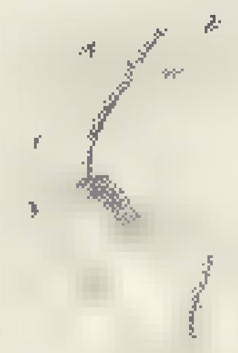

1. c


1. d

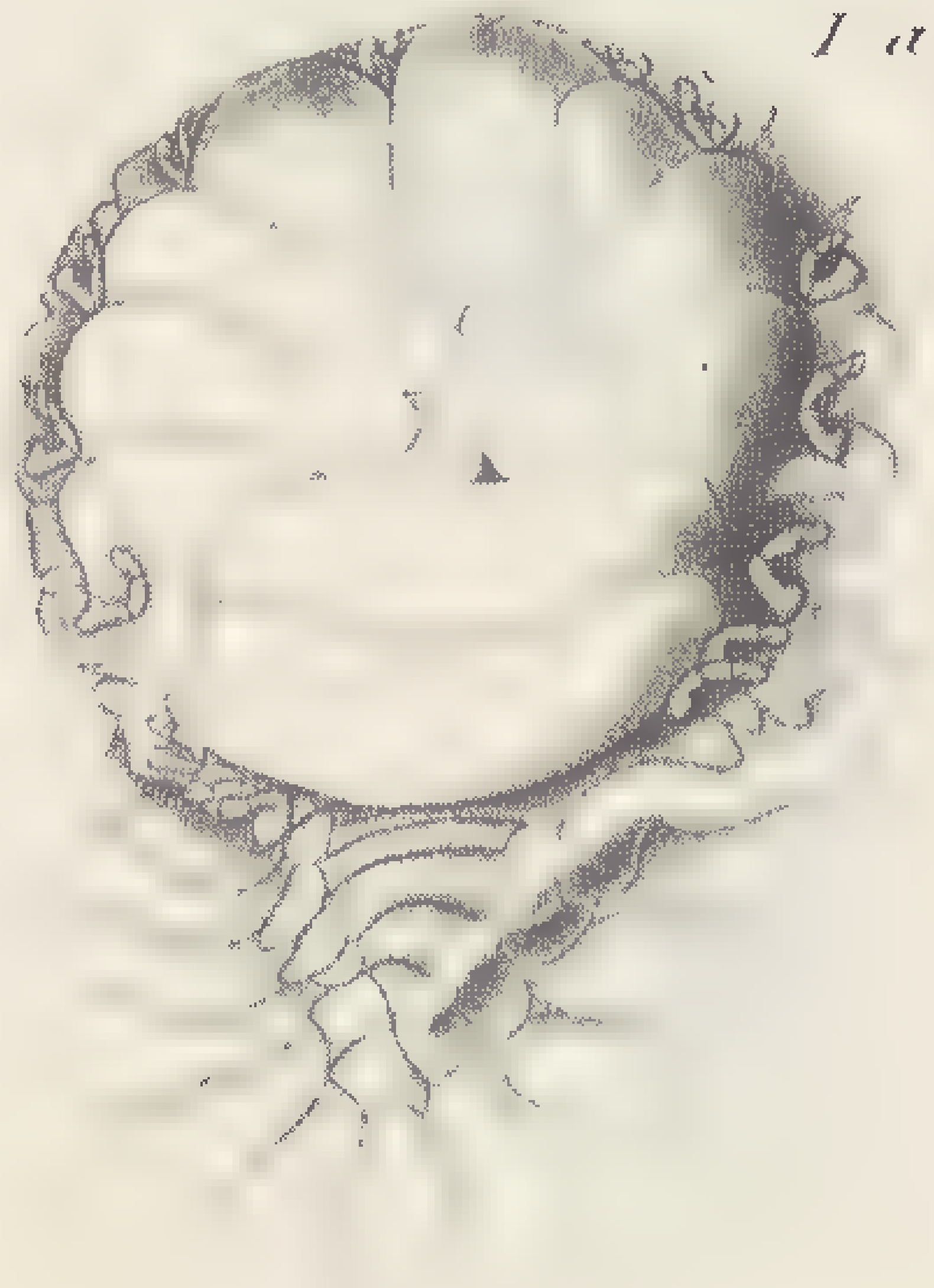

1. h

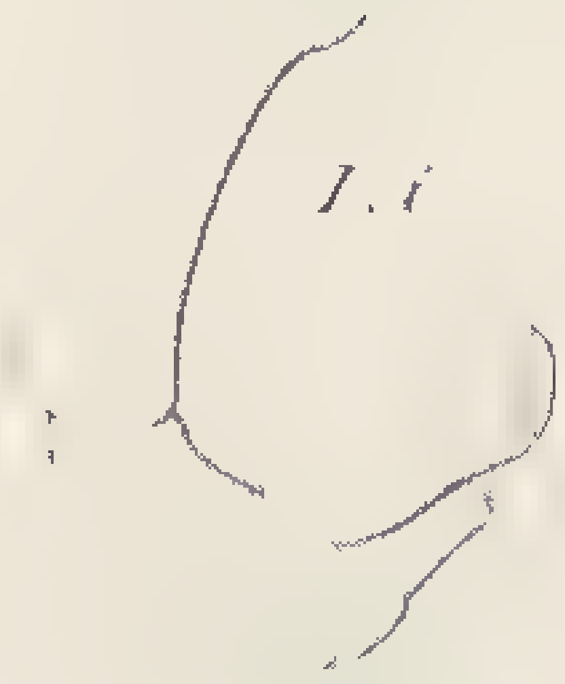
1



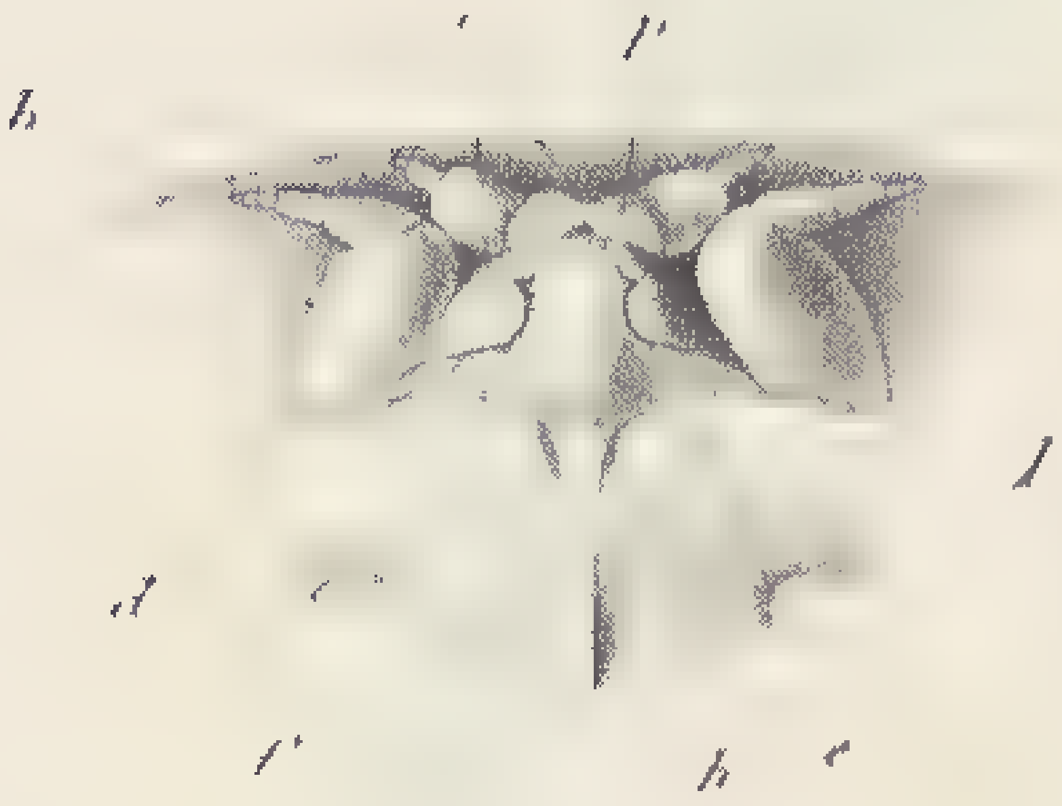

1. e

1 a




1. i

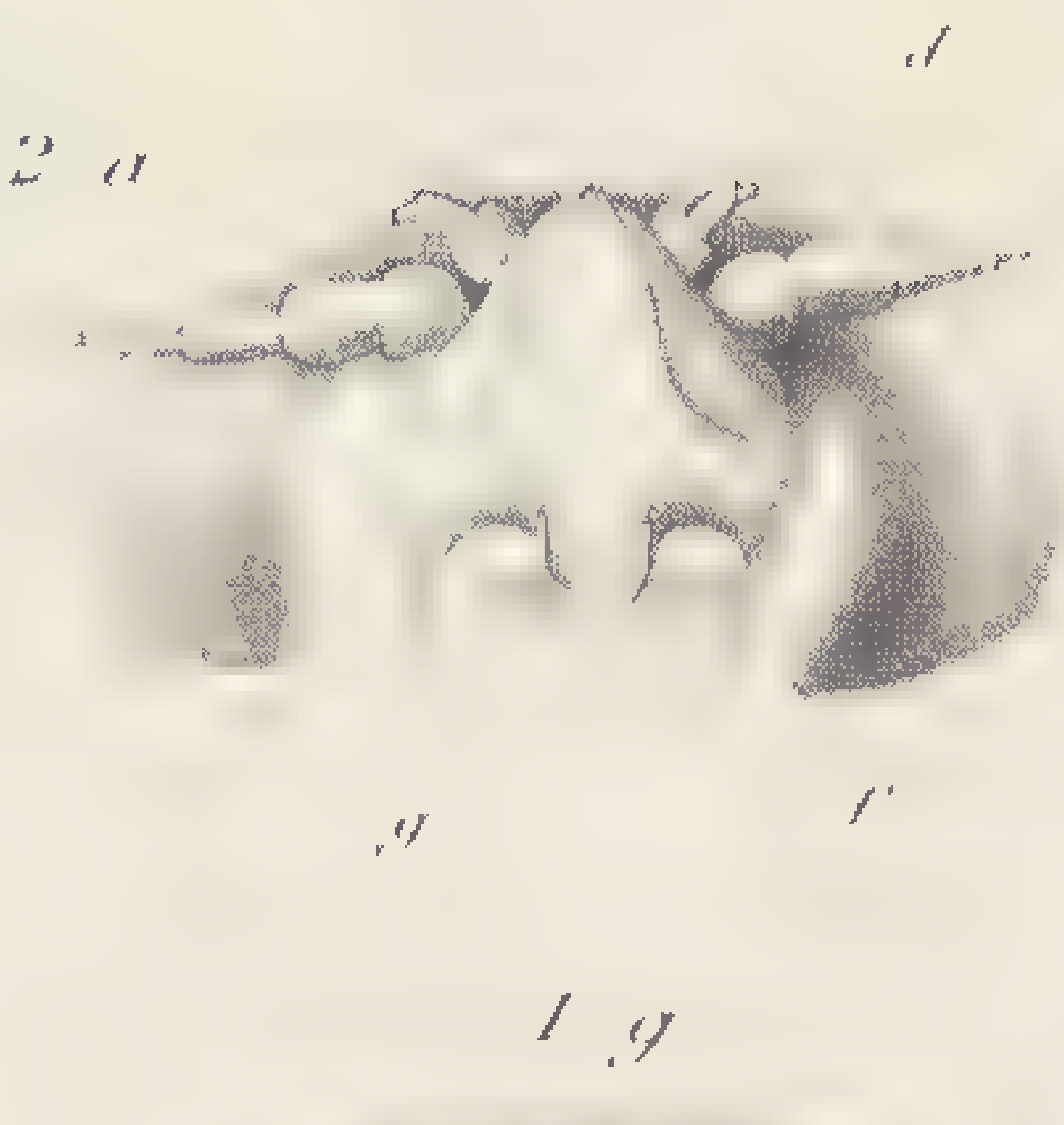
2.



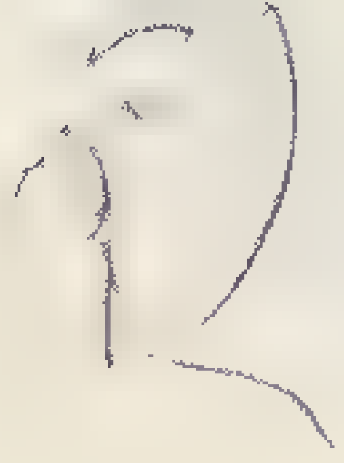
1 b

1. f

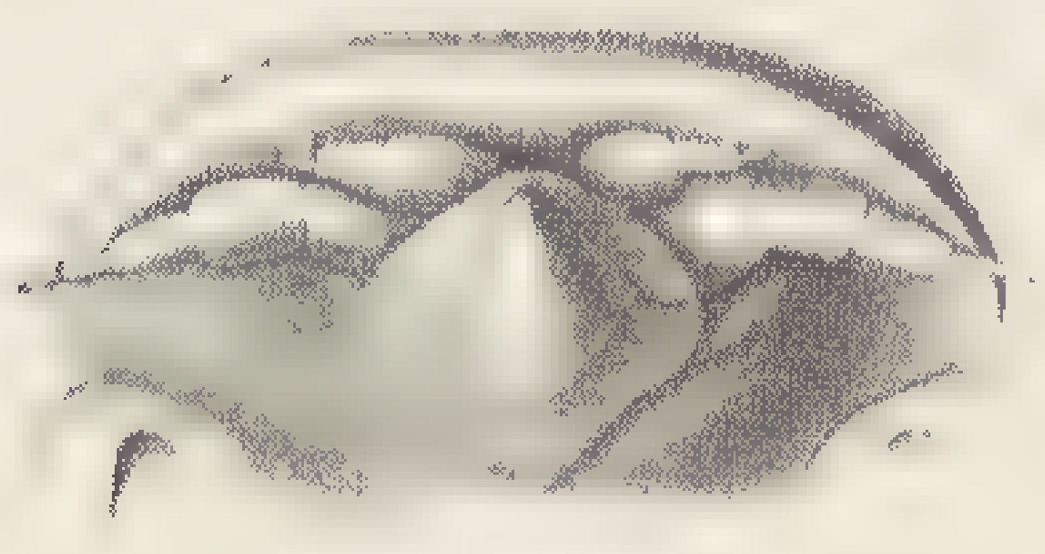
2 a



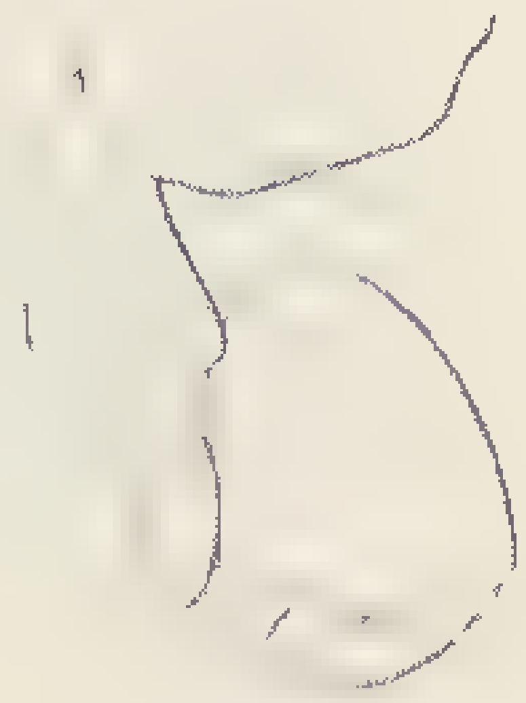
2 b



1 g



2 c



H J Hansen del

Lovendal sc

Bulletin of the Museum of Comparative Zoölogy
AT HARVARD COLLEGE.
VOL. XXXI. No. 6.

THE THORACIC DERIVATIVES OF THE POSTCARDINAL VEINS IN SWINE.

BY G. H. PARKER AND C. H. TOZIER.

CAMBRIDGE, MASS., U. S. A.:
PRINTED FOR THE MUSEUM.
MARCH, 1898.

No. 6. — *The Thoracic Derivatives of the Postcardinal Veins in Swine.* By G. H. Parker and C. H. Tozier.[1]

Introduction.

Although the postcardinal veins[2] in swine were originally studied by Rathke, and have since been reinvestigated by Hochstetter, our knowledge of them is admittedly fragmentary; for Hochstetter himself regrets that his results in the main do little more than raise doubt as to the accuracy of some of the most important of Rathke's statements, without giving grounds enough for full criticism. It is our purpose in this paper to present what seems to us a consistent account of the changes that these veins undergo, and to offer some critical comments on the questions raised by Hochstetter.

In dealing with this subject we have had recourse to the two general methods of serial sections and injection. The smaller embryos were cut into serial sections, and the courses of the veins then studied by a simple method of graphic reconstruction. The larger ones were injected with a raw starch-mass, or a celloidin-mass. In the former case the veins were afterwards dissected out; in the latter, corrosion preparations were made by dissolving away the tissues of the embryo in an artificial digesting fluid, thus leaving the courses of the vessels indicated by the celloidin. From embryos of intermediate size both reconstructions and injections were made, and the results obtained by the two methods compared.

---

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, E. L. Mark, Director, No. LXXXVII.

[2] Some little confusion exists as to the terminology of the principal veins in lower vertebrates and the homologues of these veins in mammalian embryos. The principal veins from the head of a fish are usually designated by comparative anatomists as right and left anterior cardinal veins, and their homologues in the mammalian embryo are generally named by embryologists right and left jugular veins. For these veins, whether they be in the adult fish or in the embryonic mammal, we propose to use the names right and left precardinals. In a similar way, the blood-vessels designated by comparative anatomists as right and left posterior cardinal veins, and by embryologists simply as right and left cardinal veins, will be called by us right and left postcardinals. These changes are in harmony with those by which the longer and older names, vena cava posterior and vena cava anterior, have been replaced by postcava and precava, and it is therefore hoped that they will commend themselves alike to embryologists and comparative anatomists.

Observations on Swine.

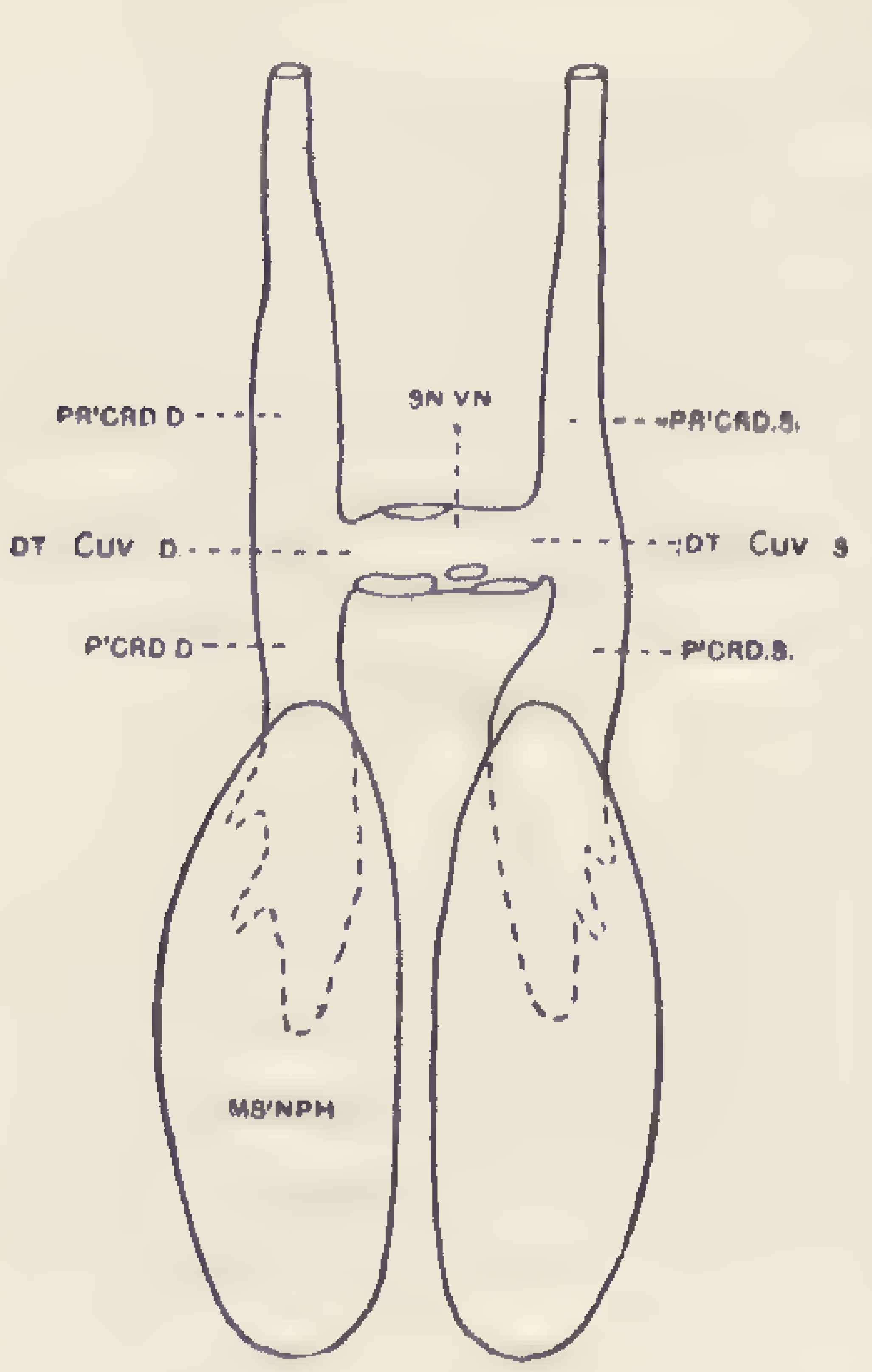


FIGURE 1.

In an embryonic pig, whose greatest length as measured in a straight line from the crown of its head to the root of its tail, was between six and seven millimeters, a reconstruction of the primary veins of the trunk, when viewed ventrally, appeared as in Figure 1. From the anterior end of the embryo, two veins, the right and left precardinals (*pr'crd. d.* and *pr'crd. s.*), pass posteriorly to the region of the heart, where each is met by a corresponding postcardinal (*p'crd. d.* and *p'crd. s.*). The pre- and postcardinals of either side unite to form transverse trunks, the right and left Cuvierian ducts (*dt. Cuv. d.* and *dt. Cuv. s.*). The ducts thus formed unite with each other, giving rise to the venous sinus (*sn. vn.*), through whose posterior wall three large veins enter from the liver, and in whose anterior wall the passage to the heart is seen.

Of these veins the postcardinals (*p'crd. d.*, and *p'crd. s.*) claim our special attention. At this stage they are symmetrical. Each begins posteriorly by a union of several small veins at the base of the hind leg of its own side of the body, and in a region dorsal and lateral to the mesonephros (*ms'nph.*) of the same side. From this region the vein extends anteriorly over the dorsal surface of the mesonephros, penetrating more or less completely the anterior end of that organ, and emerging from it to pass directly, as a well defined blood-vessel, to the Cuvierian

---

FIG. 1. Reconstruction on a frontal plane of the principal veins and the mesonephroi of an embryonic pig between six and seven millimeters long. Ventral view. × 12. *dt. Cuv. d.*, right Cuvierian duct; *dt. Cuv. s.*, left Cuvierian duct; *ms'nph.*, mesonephros; *p'crd. d.*, right postcardinal; *p'crd. s.*, left postcardinal; *pr'crd. d.*, right precardinal; *pr'crd. s.*, left precardinal; *sn. vn.*, venous sinus.

duct of the corresponding side. The partial penetration of the mesonephros by the postcardinal might with equal propriety be described as a partial intrusion of the mesonephros into the cavity of the vein, for the loosely twisted nephridial tubules hang with such freedom into the venous blood-spaces that they may with justice be said to occupy more or less of the cavity of the vein itself. This peculiar suspension of the tubules in the venous blood-spaces, a condition which persists in the later stages, has been recently noticed by Minot ('98, p. 229).

In an embryo whose greatest length (measured as before described) was between twelve and thirteen millimeters the veins just considered present the condition shown in Figure 2. Excepting for differences of size, and slight changes in outline, the precardinals are essentially the same as in the preceding stage. In the region of the venous sinus the hepatic opening, which is now single, and the anterior opening, which leads into the heart, have shifted somewhat toward the right side of the body, and the root of a coronary vein (*vn. cor.*) has been formed.

The postcardinals are very much altered. With the growth of the mesonephroi, they have become entirely interrupted in the middle part of their course; their posterior portions, however, persist near the base of the hind legs, finding an outlet toward the heart through the newly formed postcava, and their anterior portions now begin at the anterior ends of the mesonephroi, and each extends to the Cuvierian duct of its own side. The anterior portion of each postcar-

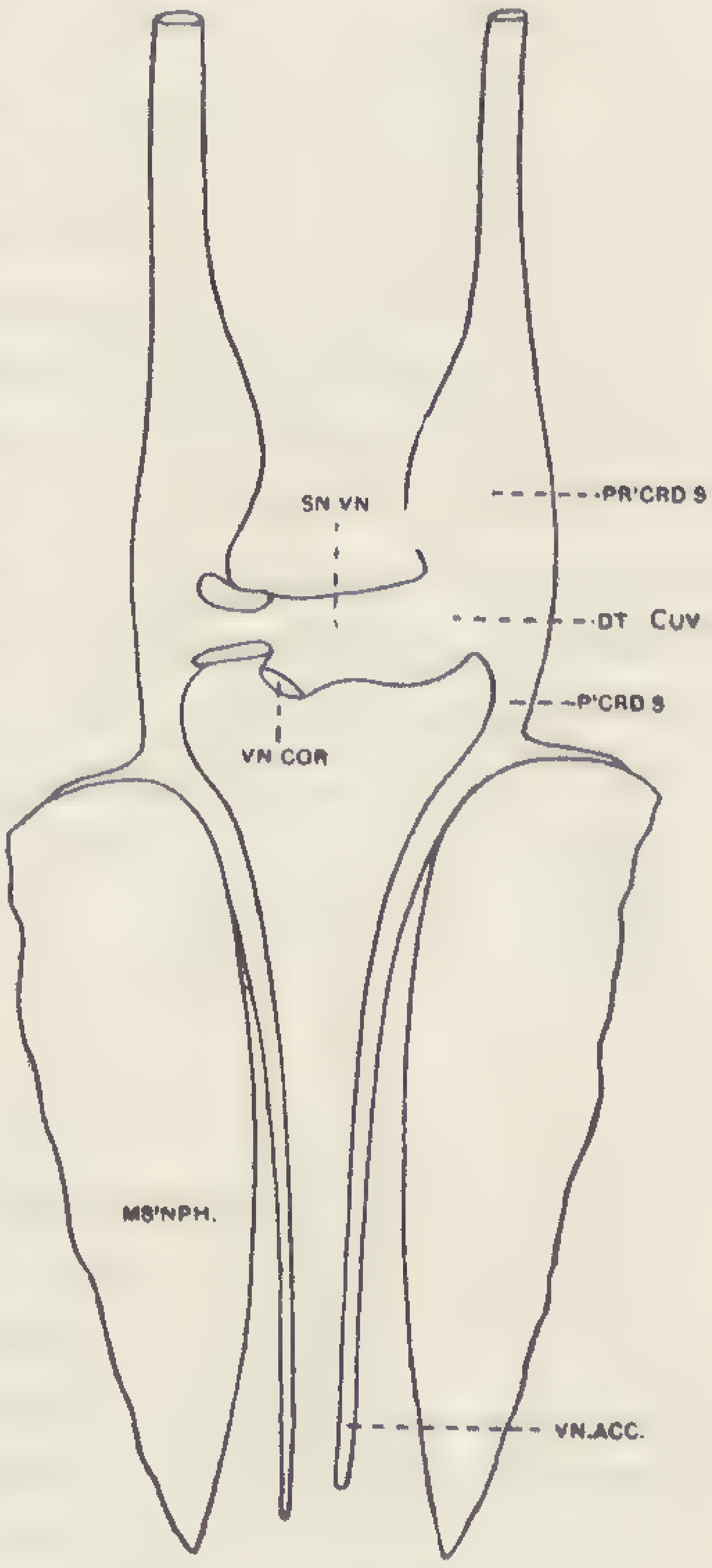


FIGURE 2.

FIG. 2. Reconstruction on a frontal plane of the principal veins and parts of the mesonephroi of an embryonic pig between twelve and thirteen millimeters long. Ventral view. × 12. *dt. Cuv.*, Cuvierian duct; *ms'nph.*, mesonephros; *p'crd. s.*, left postcardinal; *pr'crd. s.*, left precardinal; *sn. vn.*, venous sinus; *vn. acc.*, accessory vein; *vn. cor.*, coronary vein.

dinal receives blood not only from the anterior end of the mesonephros but from the region between the two mesonephroi. This is accomplished, however, not by the postcardinal proper, but by a new outgrowth that takes its origin from the postcardinal near the anterior end of the mesonephros. The walls of these new vessels, which may be called the accessory veins (*vn. acc.*), are extremely delicate; the exact places of union between them and the postcardinals is indicated not only by the general topography, but also by the rather abrupt change in the thickness of the walls where the accessory vessel meets the postcardinal. Moreover, the cavities of the accessory vessels are not freely open throughout their whole extent, as those of the postcardinals are, but are here and there partly interrupted by flattened trabeculæ. In fact, posteriorly these trabeculæ become so numerous that the cavities of the vessels are finally merged in the interspaces thus formed. The accessory vessels at this stage may be traced posteriorly to a point about midway the length of the mesonephros.

In slightly smaller embryos the accessory veins are much shorter, but even in these they always open freely into the postcardinals, and we therefore believe them to be outgrowths of the postcardinal vessels. The place of union between the accessory vessels and the postcardinals in the specimens studied was at the level of the tenth rib, and the accessory vessels could usually be traced posteriorly some distance beyond the last or fourteenth rib.

In an embryo whose greatest length was about forty-eight millimeters, the postcardinal and the accessory constituents of each vein could no longer be distinguished, for they had fallen so well into line with each other that they were represented by a perfectly continuous vein (Figure 3). That on the left side, which may now be called the hemiazygos vein (*vn. hm'az.*), retained its earlier connections and extended from the left Cuvierian duct along the left side of the vertebral column to a point some distance posterior to the last rib. That on the right side, the azygos vein (*vn. az.*), had lost its anterior connection with the right Cuvierian duct, but otherwise extended over a tract corresponding in the main to that of the hemiazygos. The blood collected

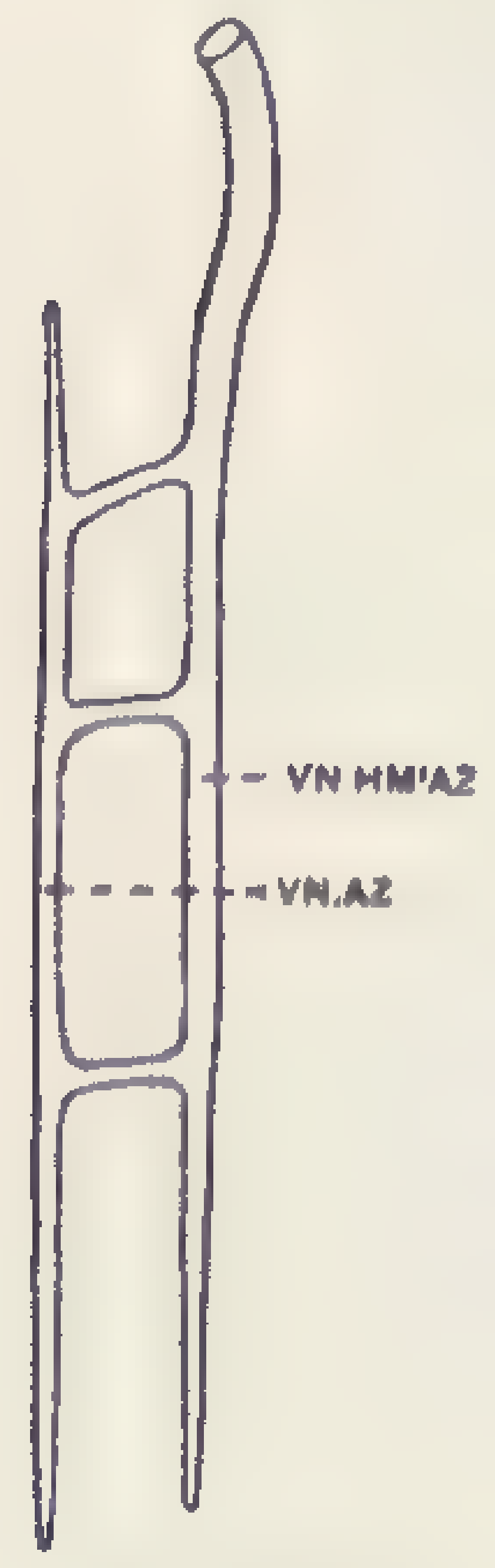


FIGURE 3.

FIG. 3. Reconstruction of the azygos and hemiazygos veins from an embryonic pig about forty-eight millimeters long. Ventral view. × 12. *vn. az.*, azygos vein; *vn. hm'az.*, hemiazygos vein.

by the azygos vein was transferred by transverse connecting vessels to the hemiazygos, by which it was carried to the heart. In the specimen from which the reconstruction shown in Figure 3 was made, three such transverse connections were found. In a specimen fifty-five millimeters long, studied by injection, five such vessels occurred, and these were so placed that their ends were opposite the mouths of the newly forming intercostal veins.

The most striking peculiarity of the stage illustrated by Figure 3 is its lack of symmetry. In the earlier conditions described these veins have been bilaterally symmetrical; but with the loss of connection between the azygos and the right Cuvierian duct this symmetry disappears, and a connection with the heart is retained only through the left side. In this respect the pig and probably all ruminants differ from other mammals, in which as a rule the azygos, not the hemiazygos, retains its original connection with the heart.

The further changes that the azygos and hemiazygos undergo may be seen in pigs ranging in length from seven to twenty centimeters. The chief features of these changes consist in the further reduction of the azygos, together with the retention of the transverse connecting vessels, by which the right intercostals are brought to connect directly with the hemiazygos. Depending upon the way in which the azygos is reduced, three types can be distinguished. These are illustrated in Figure 4.

In the first type (Fig. 4, A) the hemiazygos reaches from the heart posteriorly to the eleventh intercostal space, receiving in its course the intercostal veins on the right from the sixth to the eleventh, and on the left from the fifth to the eleventh. Posterior to the eleventh intercostals two longitudinal veins appear, which are of about equal size, and extend posteriorly two segments farther, receiving the twelfth and thirteenth intercostals. Of these the left one (*vn. hm'az.*) obviously represents the posterior continuation of the hemiazygos, the right one (*vn. az.*) the last remnant of the azygos, which in the region of the eleventh intercostal still retains its transverse connection with the hemiazygos.

In the second type (Fig. 4, B) the hemiazygos (*vn. hm'az.*) extends as the predominant vessel from the heart to the fourteenth intercostal space. The azygos is entirely suppressed, except for a small part running from the twelfth to the thirteeth intercostal and possessing at its two ends transverse connections with the hemiazygos.

In the third and last type (Fig. 4, C) the hemiazygos is a well developed trunk from the heart to the ninth intercostal, beyond which the blood is conducted in the main through what is obviously the persistent azygos (*vn. az.*), though remnants of the hemiazygos occur between the ninth and tenth right intercostals, as well as between the eleventh and twelfth.

Thus in the three types considered the anterior part of the system is always formed exclusively from the hemiazygos. The posterior part may be derived from the equally persistent azygos and hemiazygos (type one) or from a preponderant hemiazygos (type two) or finally from a preponderant azygos (type three).

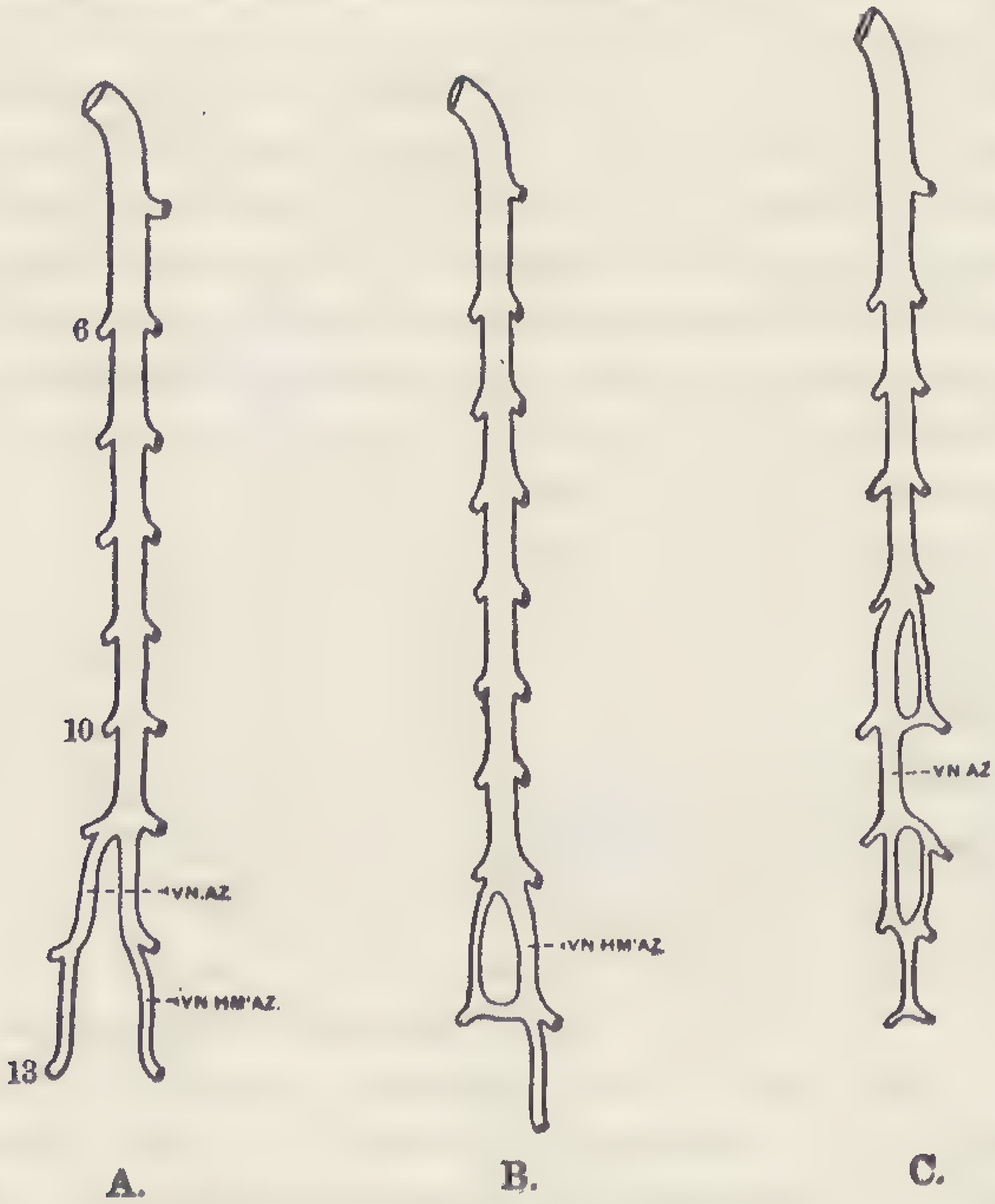


Figure 4.

Fig. 4. The hemiazygos and connected veins, showing three structural types. Raw starch injections. Ventral views. *vn. az.*, azygos vein; *vn. hm'az.*, hemiazygos vein; 6, 10, 13, bases of the sixth, tenth, and thirteenth intercostal veins respectively.

A. Type one, with equally persistent azygos and hemiazygos. From an embryonic pig about seven centimeters long. × 3.

B. Type two, with preponderant hemiazygos. From an embryonic pig about eleven centimeters long. × 2.

C. Type three, with preponderant azygos. From an embryonic pig about twenty centimeters long. Natural size.

It will be recalled from the earlier part of this description that the two components (postcardinal and accessory vein) which make up the azygos and the hemiazygos were united at about the level of the tenth rib. The hemiazygos from the region of the heart to the tenth rib is therefore to be regarded as the persistent anterior portion of the left postcardinal. As the corresponding part of the azygos has aborted, the right postcardinal of this region is entirely absent. Consequently the variable portion of this system — most of which lies posterior to the tenth, or at least to the ninth rib — represents the parts derived from the accessory veins.

Although the main stem of the hemiazygos from the heart to the region of the tenth rib has been stated to be derived exclusively from the left postcardinal, it is possible that occasionally a portion of its posterior extent may come from a fusion of both right and left postcardinals; for in one instance we found between the levels of the ninth and tenth intercostals (compare Fig. 4, C) an "island" formation which was so narrow that the right and left components may be said to have almost completely united. While the rareness of such cases makes it improbable that a process of fusion is at all usual, the possibility of its occurrence cannot be ignored, and, where fusion does occur, the incorporation of a part of the right postcardinal into what becomes the main stem of the hemiazygos is at least a possibility. Aside from this, however, the right postcardinal certainly plays no part in the ultimate formation of the system of veins under consideration.

Historico-critical Remarks.

The postcardinals of swine were first described by Rathke ('30, p. 64), whose account, though mainly taken from the sheep, applies, according to this author, almost equally well to the pig. The same account was subsequently somewhat amplified and published by Rathke ('32, p. 82) in a second paper. In both these papers the postcardinals are called posterior venæ cavæ (hintere Hohlvenen), for Rathke believed at this time that the right postcardinal persisted throughout its whole extent as the adult postcava. He further believed that the thoracic portion of the left postcardinal became the hemiazygos. This interpretation agreed well with the fact that, as Rathke ('30, p. 67) pointed out, adult sheep and pigs have no azygos veins, structures that might be supposed to represent the right postcardinals. Stark, as we gather from the historical account given by Hochstetter ('93, p. 611), subsequently showed that in embryonic sheep, in addition to a postcava, an azygos vein also occurred. Rathke seems to have become cognizant of this fact, for in his third paper on this subject he abandoned his earlier views on the fate of the postcardinals, and, without stating reasons for the change, adopted views more nearly in accordance with the new observations made by Stark.

According to Rathke's ('38, pp. 3, 4, and pp. 10, 11) later view, the anterior thoracic portion of the left postcardinal is involved in the formation of the hemiazygos, and the right postcardinal in a similar way enters into the formation, not of the postcava, but of the embryonic azygos. This view agrees in the main with the results obtained by recent investigators (Hochstetter, '93, and Zumstein, '96, '97) on other mammals, and is abundantly confirmed by our own observations on swine.

The facts thus far stated are only a partial exposition of Rathke's later opinion. Only the anterior portions of the azygos and hemiazygos are formed, according to Rathke's later view, from the postcardinals, the posterior parts being developed from a system of longitudinal anastomosing trunks between the successive intercostal veins. These anastomosing trunks receive the blood from the intercostals, passing it forward towards the heart, and thus form a longitudinal vessel, which gradually replaces a part of the original postcardinal. The extent to which this replacement occurs may be indicated as follows. The part of the hemiazygos extending from near the heart to the sixth intercostal vein represents a persistent part of the postcardinal, and the remaining part from the sixth intercostal posteriorly to the last one is a new formation from the longitudinal anastomosing vessel; the part of the embryonic azygos from its connection with the heart posteriorly to the eighth or tenth intercostal represents the right postcardinal, the remaining posterior portion having been derived from the longitudinal anastomosing vessel of that side. After the right intercostals establish transverse connections with the hemiazygos, the azygos disappears, thus leaving the hemiazygos as a return trunk for the blood from the right as well as from the left intercostals.

That the posterior portions of the azygos and of the hemiazygos in many mammals are new formations added to the remnants of the postcardinals is now, we believe, generally admitted, and, as we ourselves have seen, is certainly true for swine; but that these new formations, the accessory veins, develop from anastomosing branches between the intercostal veins, as stated by Rathke, is not, we believe, in accordance with fact. Of the several embryos examined by us at the stage in which the accessory veins were developing, no trace of intercostals or intercostal anastomoses could be discovered, but the accessory veins grew at their posterior ends by a process that seemed like the formation of an opening through the tissues independent of any pre-existing blood-cavities. We therefore believe that Rathke was in error in ascribing to the non-cardinal parts of the azygos and hemiazygos veins in swine an origin from intercostal anastomoses.

In justice to Rathke, however, it should be mentioned that longitudinal anastomosing vessels between the intercostals do occur in embryonic pigs. We have never identified these in early stages, but their presence can be easily demonstrated in older embryos by means of celloidin injections that have been converted into corrosion preparations. In a pig about six centimeters long, the veins between the ninth and eleventh intercostals, when thus prepared and viewed from the dorsal side, are represented in Figure 5. From the longitudinal hemiazygos (*vn. hm'az.*) pass off on the left the three intercostals 9, 10, and 11; on the right, intercostal 11 and intercostal 9, to which intercostal 10 is attached by a longitudinal trunk (*vn. az.*), which probably represents a part of the once complete azygos.

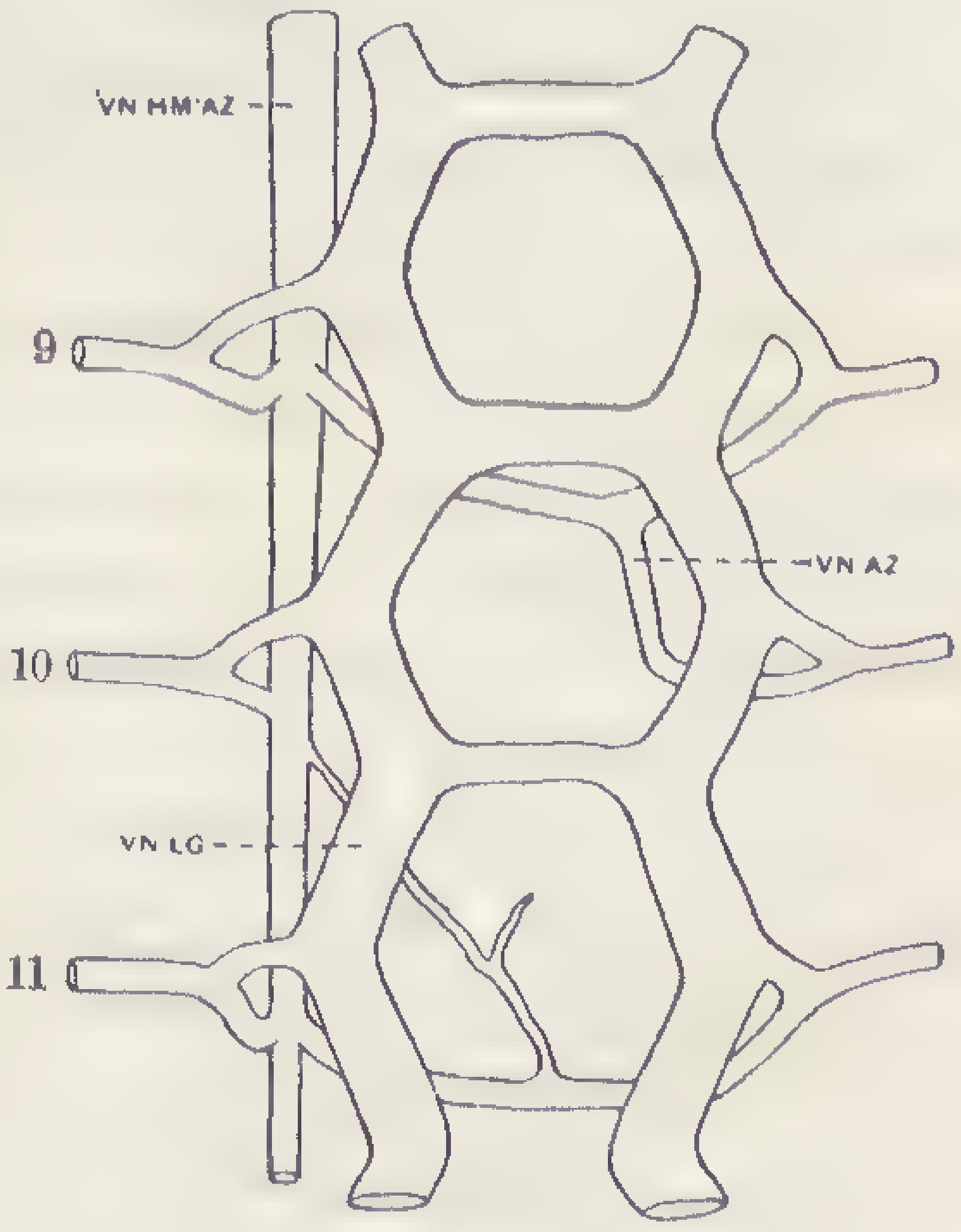


FIGURE 5.

Each of the six intercostal veins mentioned gives off a short dorsal vessel, which opens into a zigzag longitudinal trunk (*vn. lg.*) of the corresponding side of the body. Thus the intercostals of a given side are put into communication with one another by a longitudinal anastomosing trunk. The right and left anastomosing trunks are moreover connected transversely, at regular and frequent intervals, in regions where their inwardly directed angles approach each other, thus producing a series of more or less hexagonal "islands" bounded by blood-

---

FIG. 5. The hemiazygos and connected veins from the region of the ninth to the eleventh intercostals in a pig about six centimeters long. Celloidin injection freed by artificial digestion. Dorsal view. × 10. *vn. az.*, azygos vein; *vn. hm'az.*, hemiazygos vein; *vn. lg.*, longitudinal anastomosing vein; 9, 10, 11, respectively ninth, tenth, and eleventh intercostal veins of the left side.

spaces. This system of longitudinal anastomosing vessels may be traced through at least the whole length of the thorax, and lies only a little dorsal to the region occupied by the hemiazygos, being thus in the neighborhood of the forming vertebral column. It seems to us highly probable that these anastomosing vessels were the ones seen by Rathke, and supposed by him to enter partially into the formation of the azygos and hemiazygos veins, a conclusion which, though in our opinion erroneous, is nevertheless not surprising when one considers the methods of investigation employed in his time. What the origin of these vessels may have been and what their subsequent fate may be have not been determined by us, but that they contribute nothing to the formation of the azygos or of the hemiazygos we feel perfectly assured.

The development of the azygos and hemiazygos veins in swine conforms, then, in general to that found by Hochstetter ('93) and by Zumstein ('96, '97) in other mammals.

In one respect, however, there is in this connection still ground for difference of opinion among recent students; this has to do with the proportions in which the postcardinal and accessory components enter into the formation of the azygos and hemiazygos. According to Zumstein ('96, p. 601), in the human being the azygos and the hemiazygos, if there be one, are formed from the postcardinals exclusively, whereas in the Guinea pig (Zumstein, '97, p. 188) both vessels are almost entirely formed from the accessory veins. In the rabbit, and probably also in the cat, according to Hochstetter ('93, pp. 589 and 595), the plane of separation between the two components lies in the eighth thoracic segment, and this agrees very nearly with our observations on swine, where it lies near the tenth pair of ribs. These differences, which are clearly not fundamental, are more likely due to peculiarities in the development of the respective species than to errors of observation, though such topographical determinations are by no means simple.

Conclusions.

1. Small embryonic pigs possess well developed right and left postcardinals (posterior cardinal veins), which extend from the bases of the corresponding posterior extremities anteriorly over the dorsal surfaces of the mesonephroi to the Cuvierian ducts.

2. The thoracic portion of each postcardinal persists from the heart to the region of the tenth pair of ribs, beyond which a new vessel, the accessory vein, is developed to a point some distance posterior to the last pair of ribs.

3. The united postcardinal and accessory veins of the right side give rise to the azygos vein; those of the left side, to the hemiazygos.

4. The azygos and hemiazygos veins receive the intercostal veins of their respective sides and become mutually connected by several transverse veins.

5. The cardinal portion of the azygos vein usually degenerates completely, and the right intercostal veins formerly connected with it then find an outlet through the corresponding part of the hemiazygos, which persists in the adult pig.

6. The accessory parts of the azygos and hemiazygos veins may remain connected with the cardinal part of the hemiazygos, and by their variations give rise to three structural types: first, one in which both accessory parts are equally developed; secondly, one in which the hemiazygos accessory predominates; and thirdly, one in which the azygos accessory predominates.

PAPERS CITED.

Hochstetter, F.
'93. Beiträge zur Entwicklungsgeschichte des Venensystems der Amnioten. III Säuger. Morphologisches Jahrbuch, Bd. XX. pp. 543–648, Taf. XXI.-XXIII.

Hochstetter, F.
'94. Entwickelung des Venensystems der Wirbeltiere. Ergebnisse der Anat. und Entwg., Bd. III. pp. 460–489.

Minot, C. S.
'98. The Veins of the Wolffian Body. Science, N. S., Vol. VII. No. 164, p. 229.

Rathke, H.
'30. Ueber die früheste Form und die Entwickelung des Venensystemes und der Lungen beim Schafe. Arch. Anat. u. Physiol., Jahrg. 1830, pp. 63–73, Tab. I.

Rathke, H.
'32. Abhandlungen zur Bildungs- und Entwickelungs-Geschichte des Menschen und der Thiere. Erster Theil. F. C. W. Vogel, Leipzig. 114 pp., Tab. I.–VII.

Rathke, H.
'38. Dritter Bericht über das naturwissenschaftliche Seminar bei der Universität zu Königsberg. Nebst einer Abhandlung über den Bau und die Entwickelung des Venensystems der Wirbelthiere. Königsberg. 23 pp.

Zumstein, J.
'96. Zur Anatomie und Entwickelung des Venensystems des Menschen. Anat. Hefte. Erste Abt., Arbeiten. Bd. VI. pp. 571–608, Taf. XXVI.–XXXVII.

Zumstein, J.
'97. Zur Entwickelung des Venensystems bei dem Meerschweinchen. Anat. Hefte. Erste Abt., Arbeiten. Bd. VIII. pp. 165–190, Taf. XXI.–XXX.

Bulletin of the Museum of Comparative Zoölogy
AT HARVARD COLLEGE.
VOL. XXXI. No. 7.

THE SEGMENTATION OF THE NERVOUS SYSTEM IN SQUALUS ACANTHIAS.

A CONTRIBUTION TO THE MORPHOLOGY OF THE VERTEBRATE HEAD.

BY H. V. NEAL.

WITH NINE PLATES.

CAMBRIDGE, MASS., U. S. A.:
PRINTED FOR THE MUSEUM.
MAY, 1898.

No. 7. — *The Segmentation of the Nervous System in Squalus acanthias. A Contribution to the Morphology of the Vertebrate Head.*[1] By H. V. Neal.

CONTENTS.

Page
- Introduction 148
  - Criteria of Segmentation 148
  - Summary of Results of former Investigations on the Segmentation of the Encephalon 150
- I. Locy's "Neural Segments" or "Metameres" 154
  - a. Material 154
  - b. Method of Study 155
  - c. Description of Locy's "Neural Segments" 156
  - d. Continuity of the "Segments" 159
  - e. Interpretation of the Evidence 161
  - f. Limit of "Cephalic Plate" . 162
- II. The "Hindbrain Neuromeres" in S. acanthias 166
  - a. Definition of the Term "Neuromere" 166
  - b. Development of Hindbrain Neuromeres 167
  - c. Summary 172
- III. The Neuromeres in the Trunk Region 173
  - a. Development of Myelomeres 173
  - b. Summary 176
- IV. The Neuromeres anterior to the Hindbrain 177
  - a. Essential Criteria of Neuromeres 177
  - b. Development of the Forebrain and Midbrain . . . 179
  - c. Summary 185
- V. The Relation of Neuromeres to Somites 186
  - a. Relation of Myelomeres to Somites 186
  - b. Relation of Encephalomeres to Somites 187
  - c. Somatic Value of the Pre-otic Mesoderm Segments . . 187
  - d. Summary 206
- VI. The Relation of Neuromeres to Nerves 207
  - a. Historical Review . . . 208
  - b. Nerve Relations in the Trunk of S. acanthias . . 210
  - c. Nerve Relations in the Cephalic Region 211
  - d. Development of the
    - 1. Oculomotorius . . . 220
    - 2. Abducens 230
    - 3. Trochlearis 235
- VII. Segmental Value of Hindbrain Neuromeres 240
  - a. Non-phylogenetic Interpretation 240
  - b. Phylogenetic Interpretation 243
  - c. Interpretation of Hindbrain Neuromeres in S. acanthias 245
- VIII. Primitive Relations of Cephalic Segments I.–VII. . . . 254
  - a. Encephalomere VII. . . . 254
  - b. Encephalomere VI. . . . 255
  - c. Encephalomere V. . . . 255
  - d. Encephalomere IV. . . . 256
  - e. Encephalomere III. . . . 258
  - f. Encephalomere II. . . . 258
  - g. Encephalomere I. 259
  - h. Comparison with the Segmentation of Amphioxus . 260
  - i. General Conclusions . . . 268
- IX. Summary 275
- Bibliography 279
- Description of Plates 293

---

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, under the direction of E. L. Mark, No. LXXXIX.

Introduction.

Criteria of Segmentation.

Morphologists have long sought to compare in Vertebrates a head segment with a trunk segment. They have assumed that in the ancestors of Vertebrates head and trunk were differentiated from each other, and that similar segments once extended throughout the entire length of the body. Direct evidence in favor of this assumption is now furnished, it is held, by Amphioxus. Because of the many difficulties involved, the problem has become a favorite one, and since the early attempts made by the poet Goethe and anatomists of the "Transcendental" school, many men have contributed evidence and theory in the hope of its solution. Since Goethe and Oken maintained the bony cranium to be composed of fused vertebræ comparable with those in the vertebral column, the problem has passed through several phases. First, Huxley ('58), upon broad comparative anatomical evidence, proved that nothing like a vertebra is to be found in the cranium of either high or low Vertebrates, and he concluded as a result of his researches that morphologists, in attempting to find a primitive metamerism in a structure which is so late in its phylogenetic appearance as the bony cranium, were approaching the problem in the wrong direction. In thus disproving the "vertebral theory" of the Vertebrate cranium, however, "war die Frage doch noch nicht aus der Welt geschafft," as Gegenbaur wrote in his famous "Kritik." By Gegenbaur ('72) the question was transformed into a problem of the phylogenesis of the *entire* head. By using as criteria the visceral arches and the nerves which innervate them, he attempted to determine the number of primitive segments in the head of those low Vertebrates, the Selachii, which in his opinion most resembled the hypothetical Vertebrate ancestors.

With the gradual acceptance of the "fundamental law of biogenesis," that the development of an individual is an epitome of the development of the race, the evidence offered in the solution of the problem of the morphology of the Vertebrate head has become more and more embryological.

After Balfour's ('78) discovery that the primary body cavity of Selachian embryos extends unbroken into the head region, and the further discovery of Marshall ('81) that in these embryos the body cavity of the head undergoes an independent segmentation into mesodermal cavities, Selachian embryos became the chief objects of research. It was finally left to van Wijhe ('82) to demonstrate in Selachian embryos an uninterrupted continuity, and a direct morphological comparability, of head and trunk "Mesodermsegmente," and thus, in the opinion of many morphologists, the existence of an "acraniote" stage in the development of craniote embryos. Since the "mesodermal segments" or somites were regarded as the best evidence of the primitive segmentation, it was at first believed that the problem of the morphology of the Vertebrate head, as regards both number and nature of segments, had at last been solved by van Wijhe. His conclusion was that nine segments, four of which were pre-otic and five post-otic, enter into the formation of the Vertebrate head, or at least the Selachian head.

Yet one who studies the literature of the decade and a half that has elapsed since van Wijhe wrote his famous paper must conclude, from the great divergence of opinion which still prevails among the most competent investigators as regards both nature and number of head segments, that the problem is "noch nicht aus der Welt geschafft." According to Froriep, Kastschenko, and Rabl, the segments of the pre-otic and post-otic regions are of a fundamentally different kind. Furthermore, while Rabl ('92) finds not over three segments in the entire pre-otic region, Dohrn ('90) finds in the same region twelve to fifteen segments, serially homologous with trunk segments. These, indeed, represent extremes of opinion, for the majority of morphologists agree with Gegenbaur and van Wijhe that pre-otic segments are few but comparable with trunk segments. The chief causes of the present disagreement of morphologists are two. In the eager search for evidence of *segments* investigators have often failed (1) to control their results, based upon the study of a single organ system, by a comparison of the *actual* conditions which obtain in other organ systems in the same organism; and (2) to control conclusions based upon a single organism by appeal to the facts and conclusions of comparative anatomy and embryology. As the result of the healthful scepticism of such accurate observers as Froriep, Kastschenko, and Rabl, the necessity for such control now seems too obvious to need repetition here.

While morphologists (excepting Gegenbaur) in attempting to elucidate the problem of cephalic segmentation have based their conclusions chiefly on the study of the mesodermal segments, — since these have seemed to afford the best criteria of segmentation, — yet other embryonic structures have also been studied, viz. the segments of the central nervous system, or "neuromeres," the nerves, the epibranchial organs, the blood-vessels, and the visceral arches.

It is well known that in embryos of all classes of Vertebrates the central nervous system shows a segmentation which consists in a series of constrictions and dilatations extending throughout the length of the neural tube, giving to it a beaded appearance. In the trunk the nerves have a definite relation to the segments of the spinal cord, the "myelomeres," as I shall call them, adopting the term introduced by McClure ('89), and it is believed that the cranial nerves also have definite relations to the segments of the brain, the "encephalomeres," although their relations are less clear. Even if we believe with Ahlborn ('84[a]) and Froriep ('94) that the nervous system is segmented in adaptation to associated segmental structures, it is not *a priori* improbable that the number of primitive segments in the Vertebrate may be shown by the number of neural segments, for in some Invertebrate embryos segmental cephalic ganglia appear even when most other traces of mesodermal segments and related sense organs have (it is believed) disappeared.

In view of the present discrepancy between the results based upon the study of neuromerism and those based upon the study of mesomerism, it devolves upon one who attempts to elucidate the question of cephalic segmentation in Vertebrates by using the segments of the central nervous system as criteria, to show the comparability of encephalomeres with myelomeres, not only structurally, but also in relation to nervous outgrowths, and to those divisions of the mesoderm on which the segmentation of the motor nerves ultimately depends. The interdependence of motor nerve and muscle has seemed so evident that morphologists have not hesitated to make the number of cranial nerves conform with the number of somites previously determined by them. Yet the majority of investigators of the segments of the encephalon have failed to take into consideration the relation of these to the segments of the mesoderm, and consequently we find in the literature upon neuromerism a diversity of opinion such as we have learned to expect in results based upon insufficient knowledge.

Summary of Results of former Investigations on the Segmentation of the Encephalon.

The results of former investigators concerning the number of encephalomeres and their nerve relations may be summarized in the form of two tables. Table I. shows the number of segments as determined by previous investigators, as well as their relation to the primary vesicles of the brain. The total number of segments has been given in the cases where it has been stated by the observer. The observations of

Table I. — ENCEPHALIC SEGMENTS.

				F.B.	M.B.	H.B.	Total.
MAMMALS.	'42	Bischoff . . .	Dog			6	
	'69	Dursy . . .	Ox		3 ?	6	
	'77	Mihalkovics .	Rabbit			5–6	
	'86	Kupffer . . .	Sheep, Mouse, Man			5	
	'89	Prenant . . .	Swine			5	
	'91	Zimmermann .	Rabbit	2	3	8	13
	'92, '92^{a}	Froriep . . .	Mole	2	3	7	12
	'95	Broman . . .	Man			7	
BIRDS.	'55	Remak . . .	Chick			5–6	
	'77	Mihalkovics .	"			5–6	
	'85	Rabl	"			6–7	
	'87	Béraneck . .	"	2	1	6	9
	'89	Platt	"	1	1	6	8
	'90	McClure . .	"	2	2	6	10
	'91	Zimmermann .	"	2	3	8	13
REPTILES.	'84	Béraneck . .	Lizard			5	
	'87	Orr	"	2	1	6	9
	'85, '89	Hoffmann . .	"			7	
	'85, '89	Hoffmann . .	Tropidonotus . .			7	
	'90	McClure . . .	Lizard	2	2	6	10
	'91	Clarke . . .	Alligator			5	
	'92	Herrick . . .	Snake			5–7	
AMPHIBIANS.	'75	Goette . . .	Bombinator . . .			?	
	'86, '93	Kupffer . . .	Salamandra . . .	5	3	?	
	'90	McClure . . .	Amblystoma . .	2	2	5	9
	'91	Waters . . .	" . . .	3	2	5	10
	'92, '92^{a}	Froriep . . .	Salamandra . . .				4
	'92, '92^{a}	Froriep . . .	Triton				5
	'92	Wiedersheim .	Salamandrina . .	?	?	?	?
FISHES.	'75	Dohrn . . .	Teleostei			8–9	
	'84, '85	Kupffer . . .	"		3	5	
	'87	Scott	Petromyzon . . .		3	5	
	'89	Platt	Salmon			5	
	'91	Waters . . .	Cod	3	2	6	11
	'91	Zimmermann .	Acanthias	2	3	8	13
	'93	Kupffer . . .	Acipenser	5	3	5	13
	'94	Kupffer . . .	Ammocœtes . . .		3		
	'94	Locy	Squalus	3	2	6	11
	'95	Locy	"	3	2	6 (8)	14–15

investigators upon neuromerism have been seldom, if ever, so far extended as to determine the number of segments finally included in the head. The reason for this has been that the hindbrain neuromeres disappear before their relations to the posterior limit of the cranium can be determined. Table II. gives the nerve relations in different Vertebrates,

Table II. — ENCEPHALIC SEGMENTS AND NERVE RELATIONS.

			F.B.			M.B.		H.B.								
	No. of Segmental Divisions.		1	2	3	1	2	1	2	3	4	5	6	7	8	9
'84	Béraneck . .	Lacerta							V		{ VII VIII }	Ear	IX ?			
'87	Béraneck . .	Chick	I	II			III	IV	V	V	“	VI	IX			
'87	Orr	Lizard	I	II			III	IV	V	VI	“	Ear	IX	X		
'89	Hoffmann . .	Lizard						IV	V		“	“	IX	X–XI		
'89	McClure . . .	Chick	I			III	IV		V		“	“	IX	X		
'89	McClure . . .	Lizard	I			III	IV		V		“	“	IX	X		
'89	McClure . . .	Amblystoma . .	I			III	IV		V		“	“	IX	X		
'89	Platt	Salmon							V		“	“	IX			
'89	Platt	Chick							V		“	“	IX			
'91	Waters . . .	Cod	I	II		III	IV		V	VI	“	“	IX			
'91	Waters . . .	Amblystoma . .	I	II		III	IV		V	?	“	“	IX			
'91	Zimmermann .	Rabbit	I			III		IV	V		“	VI	IX	X	XI	XII
'91	Zimmermann .	Chick	I			III		IV	V		“	VI	IX	X	XI	XII
'91	Zimmermann .	Acanthias . . .	I			III		IV	V		“	VI	IX	X	XI	XII
'92	Herrick . . .	Snake							V	VI	“		IX	X		
'92ª	Froriep . . .	Mole							V	V	“	Ear	IX	X		
'95	Locy	Squalus . . .	I	II	III	IV		V	V		VII	VIII	IX	X	X	X
'95	Broman . . .	Man					IV			V	VI	{ VII VIII }	IX	X	XI	XII

so far as they have been studied. In both tables it has been impossible to exclude much that is theoretical, and in view of this fact general conclusions are obviously dangerous. One important result, which should be borne in mind during the discussion of the evidence presented in this paper, is established, viz. the constancy, in all classes of Vertebrates, of five "hindbrain neuromeres" ("Falten" or "vrais replis"), and of their nerve relations. When *six* have been counted, usually the Anlage of the cerebellum has been included with them, and when *seven* (see Hoffmann, '90), another fold behind the true fifth neuromere has been counted. There is consensus of opinion that from the third "hindbrain neuromere" (designated in Table II. as 5, and as V in my figures) the acustico-facialis nerve takes its origin. In counting hindbrain neuromeres, then, this may safely be used as a check. In regard to the presence of true neuromeres, comparable with those of the hindbrain, in the region of the encephalon anterior to the hindbrain, much is theoretical, and, as I believe, uncritical. Morphologists have naturally been more or less prejudiced in favor of the view that a serially homologous segmentation extends throughout head and trunk. This preconception has led to the search for resemblances at the risk of disregarding differences which obviously exist, and as a result structures in the encephalon which are morphologically incomparable with the myelomeres have been homologized with them. Moreover, this has been done in utter disregard of their relations to the segments of the mesoderm.

The study of neural segments and their relations to nerves and somites in embryos of Squalus acanthias has given me some facts bearing on the problem of cephalic segmentation, which are, so far as I know, new. The conclusion which I have reached is as follows. *In S. acanthias there exists in early stages a continuous primitive segmentation of the nervous system serially homologous throughout head and trunk, — the "neuromeric" segmentation.* In later stages there appears in the encephalon a secondary (in time) segmentation resulting in the so called vesicles, which are not serially homologous with the segments of the myelon, but give rise to an anterior cephalic tract, which is a region *sui generis.*

In the following discussion I propose (1) to trace the development of neuromeres; (2) to compare the structure of the segments of the encephalon with those of the myelon; and (3) to note the relation of the neuromeres to the sensor and motor nerves, to the mesodermal somites, and to the visceral arches. I shall begin with the description of the first appearance of neural segmentation in the embryo.

I. Locy's "Neural Segments" or "Metameres."

a. MATERIAL.

Much of my material was collected with a view to the study of the "neural segments" or "metameres" described by Locy ('94 and '95). In a preliminary paper, which appeared with numerous illustrations in the "Anatomischer Anzeiger," 1894, Locy affirmed the discovery of "neural segments" in embryos of Squalus acanthias[1] at stages preceding the formation of the medullary folds and "before the mesoblast has, to any extent, become divided into somites." He therefore believed that these "epiblastic segments must be independent of any formative influence of the segments of the mesoblast." This discovery is interesting, and, if confirmed, one of most fundamental importance. I have therefore collected a large number of Squalus embryos in early stages of development, in order to confirm, if possible, Locy's results.

S. acanthias is abundant along the coast of Massachusetts in early summer, and the embryos are very easily obtained. My collecting was done at Rockport, Massachusetts, during the months of July and August, 1894, 1895, and 1896, and the number of specimens obtained exceeds twenty-five hundred. Locy has well insisted on the necessity of abundant material in closely connected stages of development.

The killing agents which I have used were (1) Davidoff's corrosive sublimate-acetic; (2) Kleinenberg's picro-sulphuric (undiluted); and (3) a mixture of Kleinenberg's picro-sulphuric (1 vol.), with ½% chromic acid (3 vol.), especially recommended by Locy.

In this material were more than two hundred and fifty embryos corresponding to Balfour's stages C, D, and E. The specimen which shows Locy's "neural segments" best was killed in Kleinenberg's picro-sulphuric mixture (Plate **1**, Figs. 1 and 2). I cannot recommend the mixture composed of picro-sulphuric and chromic acids, since specimens killed in it were not well preserved histologically. Davidoff's corrosive sublimate-acetic seems to me the best for general purposes of all the killing agents I have used, and consequently most of my material has been so killed. For the special study of the development of the nerves and the fibre courses in the wall of the brain, I have used material killed with vom Rath's fluid, followed by pyroligneous acid. This method I regard as most valuable, since with it nerve fibres are differentiated by the precipitation of osmium in the very earliest stages of development, and it has given me results which I have been able to obtain in no other way. For staining sections Kleinenberg's hæmatoxylin has been used chiefly, while Heidenhain's iron hæmatoxylin and Grenacher's alcoholic borax carmine have both given excellent results.

---

[1] Squalus acanthias (Linnæus, 1748), synonymous with Acanthias vulgaris (Risso, 1826).

b. Method of Study.

In studying Locy's "neural segments" in Squalus embryos, reflected light was used, and in consequence low powers of the microscope were necessary. I have used constantly a small Zeiss stand in which the upper half of the stage and the superstructure revolve on the lower half of the stage, and his objective A and ocular I. My method of procedure has been, first, to make with the aid of a camera lucida an outline of the embryo cleared in clove oil and viewed as a transparent object. The irregularities of the edge of the neural plate may thus be represented accurately, and may serve as landmarks in the subsequent study of the specimen as an opaque object. After the outline drawing has been made, the specimen is transferred to a watch glass filled with alcohol. Now the important question is illumination. In order to bring out the delicate structures along the edges of the neural plate, oblique illumination should be used, since it brings into strong contrast the shadows and the high lights. The embryos should be rotated, so that light may be obtained successively from all directions and thus the chance of deception by false lights avoided. As the embryo is studied chiefly from the ventral side (for reasons given by Locy), careful manipulation with brush and needle is necessary in order to remove the yolk, which would otherwise obscure the edges of the neural folds. In studying these surface conditions, I have found a very faint hæmatoxylin stain and a black background to be of advantage.

In representing the specimen under observation, I have not had recourse to photography, but have made as faithful a representation as possible with pencil, seeking to preserve the relative values of light and shade. Since it is possible by careful illumination to increase the contrast of light and shade to a considerable amount, it is well to study the same embryo with different kinds of illumination. In this way it is possible to determine more satisfactorily what is permanent and what is not. The study of the segments is by no means easy, and the labor is considerable because it is necessary to study so many individuals. It is evident from a comparison of Locy's photographic representations, given in his final paper ('95), with his drawings, that the latter are, probably for the sake of clearness, semi-diagrammatic in character. While his photographic reproductions show absolutely no segmentation in the early stages, his drawings on the contrary show in these same stages "segments" as clearly marked as those of later stages. Photography is obviously unsatisfactory as a means of reproducing these delicate structures.

Before taking up the consideration of the evidence which I have obtained from my studies, it is well to give a brief review of Locy's results. In his final paper ('95) he qualified his statement that the segmentation is solely epiblastic, since he discovered in sections that it may be found in both mesoderm and ectoderm. He therefore concludes that the segments seen in surface study are the remnants of a primitive metamerism of the Vertebrate body. The more important points in Locy's description may be briefly summarized as follows. The evidence of segmentation appears first in the non-axial part of the embryo, i. e. along the thickened blastodermic rim. The segments later extend along the lateral margin of the neural plate from the anterior unsegmented tip of the embryo backward into the non-axial part. The segments are most clearly seen in "marginal bands along the neural plate," though "in the trunk region the lines of division may be traced inward toward the median furrow. This is probably due to the appearance of the mesodermic somites in that region." The "marginal bands," he thinks, "represent the dorsal nerve cord."[1] "These segments, once established in this very early stage, may be traced onward in an unbroken continuity until they become the neuromeres of other observers, and sustain definite relations to the spinal and cranial nerves." In the conclusion of his preliminary paper Locy writes, "No one is likely to question but what the segmented condition I have described represents a survival" (i. e. of an ancestral segmentation?). My own observations on embryos of S. acanthias lead me to question in large part the accuracy of Locy's observations, as well as his interpretations.

c. Description of Locy's "Neural Segments."

I shall now give an account of the conditions, as I have found them, in the head region of a shark embryo with 6 to 6½ somites.[2] This

---

[1] In his final paper Locy speaks of the "neural folds or ridges" as "divided throughout their length into a series of segments."

[2] I count the somites beginning with van Wijhe's 7th somite (somite 7 of my figures), the myotome of which becomes the first segment of the lateral trunk musculature (van Wijhe).

stage has been selected to begin with, because it gives the strongest evidence that I have seen of a segmented condition in the neural plate. I shall describe first two embryos which represent fairly well the conditions I have found at this stage. These two embryos are represented in Figures 1, 2, and 3, Plate **1**. The neural or "medullary" plate is seen to be a spatula-like expansion of the anterior end of the embryo, raised somewhat above the blastodermic area. Figure 1 (Plate **1**) represents an embryo viewed from the dorsal side; the neural plate, it will be observed, is not perfectly flat, for its edges bend slightly ventrad and a shallow depression extends along its median portion. The chorda, lying in the axis just beneath the neural plate, causes a slight elevation of the floor of the groove in the median line. Anteriorly the chorda passes into the common tissue which later becomes differentiated into entoderm, mesoderm, and chorda. The anterior more expanded portion of the neural plate has been called the "cephalic plate." At the posterior portion of this cephalic plate its lateral wing-like expansions undergo their greatest bending ventrad. The posterior or trunk portion of the neural plate extends back into the tail folds and along the embryonic rim. I do not wish to seem to imply by this statement that the tail folds and the embryonic rim become included in the neural tube, because, although in general I believe in the concrescence theory, I do not find in the *continuity* stated above any evidence of addition to the posterior part of the neural plate by a concrescence of the tail folds and the embryonic rim.

In the dorsal view of the embryo shown in Figure 1, Plate **1**, little or no evidence is afforded in either cephalic or trunk regions in support of Locy's contention that the edges of the neural plate are segmented. We see only that the edges of the plate are slightly and *irregularly* lobed, and not in the true sense segmented. For *the lobes on the opposite margins of the plate do not correspond in number or position, neither do they show any definite relation to the mesodermal somites, as seen in the cleared specimen.*

Figure 2, Plate **1**, shows the same embryo viewed from the ventral side, and gives the strongest evidence I have seen of Locy's interpretation of the condition of the neural plate. The "segments" appear much more marked in embryos of this stage when viewed from the ventral side, for reasons already stated by Locy, who has well insisted upon the importance of ventral views. There are several reasons, however, for regarding the structures which appear along the edges of the neural plate as not true segments. These so called segments, even in the cephalic region, are not equally distinct, it being very difficult, if not impossible, to determine the boundaries of some of them. They also differ considerably in length and apparently without any regularity, a condition not easily reconciled with the interpretation of them as true segments. It would certainly be impossible even in this specimen to point out with certainty corresponding segments on opposite sides of the cephalic plate. In the trunk region of the same specimen no correspondence between somites and "neural segments" is seen. However, a faint lobing of the inner margin of the tail fold is seen on the right side of the embryo. Locy's ('95, p. 519, Fig. 29) description of a stage as close to this as any figured by him is as follows: "They [the segments] appear like a row of beads running along the ventrally recurved margin, and extend with great distinctness the entire length of the embryo. Those in the trunk region are continuous with those of the head, and pass into the latter without any transition forms. There is, however, some individual variation in size of the neuromeres, and they are not absolutely symmetrical on the right and left sides, but the significant thing is, [that] there is uniformly the same number on each side in a given region, such as the hindbrain, or the brain region as a whole. . . . There seems now to be a natural landmark separating the 'cephalic plate' from the rest of the embryo; this is an abrupt downward bending in the medullary folds, which, as I have determined, lies just in front of the future origin of the vagus nerve. There are eleven *metameres*[1] in the lateral margins of the cephalic plate, including the ones embraced in this fold." The accuracy of this conclusion I shall discuss in treating of the question of the limit of the cephalic plate (p. 162). I wish here only to call attention to the fact that none of the reproductions of Locy's photographs, with two possible exceptions (his Figs. 2 and 23), show a segmentation of the neural folds in either the trunk or the embryonic rim.

If now we turn to Figure 3 (Plate **1**), we find an embryo of about the same stage as that shown in Figures 1 and 2; at least, it has the same number of somites (6 to 6½). The conditions are these. The "segments" at the margin of the neural plate differ markedly in distinctness, and are irregular in size. In the region of the cephalic plate — the posterior boundary of which is marked by the arrow — the number of segments on the right and left sides is not the same. I was not able to assert this with so much confidence in regard to the embryo of Figures 1 and 2, since in that embryo the limits of the cephalic plate were less clearly defined. If the segments of the two sides of the neu-

---

[1] Italics mine.

ral plate in Figure 2 do not admit of a satisfactory comparison, neither is it possible, even with a prejudice in favor of finding uniform conditions, to state exactly which segments of Figure 3 correspond to those of Figure 2.

An examination of many embryos (more than fifty) in this stage of development — at which, in agreement with Locy, I have found that the segments are more clearly marked than at any other stage — has served only to establish the opinion that there is no constancy in their number in different individuals, nor agreement in number or position upon the two sides of the plate of a single individual. After an examination of a large number of embryos at this and closely related stages, I have been compelled to abandon my first opinion, which was based chiefly on the study of the embryos of Figures 1 and 2, and was favorable to Locy's contention. In no case that I have seen do the segments appear symmetrical, and in no case have I been able to determine a definite relation with the somites.

d. Continuity of the "Segments."

My observations have of course not been confined to this most favorable stage. While the evidence given above, based on the study of embryos at a stage when the segments are most plainly seen, appears to my mind satisfactory proof that true segments do not exist at this time, the study of embryos in both earlier and later stages shows that even these segments are only transitory structures. This evidence, though in a sense negative, is not without weight in the treatment of the question. It constitutes, it is true, neither proof nor disproof of the genuineness of the segments. It is, however, what we should expect, if we find the segments unlike in number and size on the two sides of the same embryo and in different embryos of the same stage. A want of continuity in successive stages is not, however, what we should expect if we were dealing with true segments. These structures would certainly have much less morphological value than is assigned to them by Locy, were they simply transitory and without definite relation to organs which appear in later stages. Locy believes that he has traced them "up to the time when they form neuromeres," but he by no means makes it clear how structures which appear "like beads" along the edges of the neural plate become transformed into *ventral* structures such as, according to his own account, the "neuromeres" are. "In the trunk region," he says ('95, p. 516), "the lines of division may be traced inwards toward the median furrow. This is probably due to the appearance of the mesodermic somites in that region." In the head region, where somites do not similarly press upon the neural plate, it still remains for Locy to show how structures morphologically dorsal, as his "neural segments" are, become converted into structures morphologically ventral as well as dorsal, as are the "hindbrain neuromeres," for example.

My own evidence of their continuity in time is, as I have said, negative. Figure 4, Plate **2**, represents an early stage with three or four somites. One sees the "marginal bands" of which Locy has spoken, but only the faintest traces of segments are visible. On one side — the right — they are exceedingly irregular. At this stage the lateral edges of the neural plate are not flexed ventrally, and such segments as are to be seen at all show best from the dorsal side. A quite regular segmentation is seen on the left side of the cephalic plate, yet the segments are by no means all of the same size or distinctness, nor do they equal in size the mesodermal segments. In the trunk region the lobes of the edge of the neural plate show no definite relation to the mesodermal somites, the boundary between two somites coinciding in some cases with the depression between lobes, in others with the apices or with other parts of the lobes. I wish to call especial attention to the fact that here, as in the embryos shown on Plate **1**, *the segments are confined to the marginal bands*, and therefore do not extend into the median plate. Here, again, there is a considerable discrepancy between Locy's observations and my own.

I have found it impossible to trace definite segments into the later stages, for in these stages, before the closure of the neural tube, in the majority of specimens little or no evidence of segments along the cephalic plate can be seen.

Two embryos in later stages of development are seen in Figures 5 and 6, Plate **2**. There is practically no evidence of segmentation or lobing of the edge of the medullary folds. The segments which Locy has numbered 1, 2, and 3 are visible in many specimens, in some very distinctly, as shown in his photographs; but behind them there is an irregularly sinuous or entirely smooth edge, as shown in my Figures 5 and 6, and in Locy's photographic reproductions. These three anterior segments, according to Locy, shift their position. Since, however, I do not find them constant in appearance and position, I have not been able to regard them as of morphological importance. It is worthy of note that they appear in the region of the neuropore, and that possibly they may be partly accounted for as the result of the difficulty of fusion of the neural folds at this point (the angulus terminalis). Their late appearance is possibly also to be correlated with the late appearance of the anterior portion of the neural crest.

The evidence which I have given leads me to conclude that the so called neural segments cannot be traced into the "neuromeres" of later stages. Of the accuracy with which Locy has traced them I shall have more to say, when I speak of the limits of the cephalic plate.

e. INTERPRETATION OF THE EVIDENCE.

Locy interprets the "neural segments," as has already been stated, as "survivals of a primitively segmented condition of the body." In search for evidence to support this phylogenetic interpretation, he has studied the early stages of the Torpedo, Amphibians, and the chick.

Torpedo embryos (p. 531) are found to be "not so favorable for the study of the segments as Acanthias," yet "the number [of folds] in a given region in Torpedo corresponds to that in Acanthias." In the three Amphibian forms which Locy has studied (Amblystoma, Diemyctylus, and Rana) "there are *about* ten pairs of segments in the broadly expanded neural folds of the head." In the chick, "there are eleven segments in front of the first formed protovertebræ." Locy has also found (p. 539) that in the chick *"the walls of the primitive groove are also divided into segments that are similar to those that appear in the neural folds."* [1]

Owing to the evidence stated above, I am unable to regard the segments in S. acanthias as of phylogenetic value. Are they then artifacts, as suggested by Eycleshymer?[2] I do not think so. Several of the best fixing agents have been used by Locy and myself, and he has in addition observed these structures in living embryos. It is known, however, that different fixing agents cause differences in internal and external conditions, as the result of swelling or contraction. They may have served to intensify the distinctness of Locy's segments, yet it is hardly probable that they are the sole cause of them.

I believe that the segments are the results of unequal growth along the margin of the neural plate. It is obviously not necessary to

---

[1] Italics my own.

[2] Eycleshymer's ('95, p. 394) observations on Amblystoma do not agree with those of Locy. Eycleshymer states that "certain markings which might be interpreted as neuromeres are often observed in the neural folds, yet their arrangement is decidedly irregular, and one is led to believe that they indicate nothing more than artifacts caused by the killing agents." I have carefully examined Amblystoma embryos, at a stage when the neural folds are widely open, and my observations agree with those of Eycleshymer.

regard such irregularities of the edge of a rapidly expanding plate of tissue as of morphological importance. It is very significant that the segments show most prominently in the cephalic-plate region just before the edges of the plate begin to rise dorsally, for it is likewise at this stage that I find the first evidence of the disassociation of cells along the edges of the neural crest. Such a disassociation of cells, or even a rapid proliferation of cells, — which certainly does occur in this region, — would lead to such phenomena as those reproduced in Figures 1 and 2, Plate **1**. An examination of cross sections of the cephalic plate (Plate **7**, Figs. 55 and 56) before the edges have fused dorsally to form a closed tube shows that the neural crest is already differentiated from the tissue which will form the walls of the neural tube; it is differentiated as a region of rapid cell proliferation and of less compactly arranged nuclei. If the centres of cell proliferation were fixed, then we should have a segmented neural ridge, as affirmed by Beard ('88).

My interpretation differs from Locy's, since he finds the "neural ridges" segmented regularly, and considers the segments as survivals of an ancestral segmentation; whereas I find the edges of the neural plate irregularly and somewhat transitorily segmented, the irregularity and inconstancy of the segments precluding, in my opinion, a phylogenetic interpretation. Locy's results from surface studies seem to me to be a confirmation of those reached by Beard ('88), who, in studying the development of the peripheral nervous system in Selachii, found from the examination of sections that the neural crest is differentiated before somites appear, and that it is from the beginning segmented. Beard's conclusions have, however, never been confirmed, and have indeed been regarded by Dohrn ('90, p. 55) as quite untenable.

To demonstrate that Locy has not accurately traced the "neural segments" onward in unbroken continuity until they become the "neuromeres of other observers," I propose to discuss the relation of the neuromeres to the posterior limit of the cephalic plate.

f. Limit of "Cephalic Plate."

Locy ('95, p. 543) has stated that in early stages of the embryo, before the neural plate has formed a closed tube, head and trunk may be distinguished. "It is possible," he says, "in very young stages to draw a line indicating where the expanded part of the cephalic plate joins the nonexpanded part of the embryo. . . . This is, in Squalus acanthias, just in front of the point where, subsequently, the vagus nerve begins. . . . In this animal, we may identify that part of the head which lies in front of the vagus nerve by counting the first eleven neural segments. It will be merely a question of agreeing upon the number of primitive segments belonging to the vagus, to enable us to locate with definiteness the hindermost limit of the head. Besides being of use in other ways, this would enable us to say, even in the earliest stages, what is head mesoblast and what is trunk mesoblast."[1]

I cannot see that Locy's determination of the limits of the cephalic plate helps us at all in the determination of the boundary of head and trunk. This boundary, as he states, has still to be determined. To fix the limits of head-mesoderm by a direct study of the mesoderm itself is quite as easy as to determine its boundary by the still hypothetical posterior boundary of the vagus region. According to Locy, the posterior limit of the cephalic plate separates neither what is pre-otic from what is post-otic, nor head from trunk.

My own observations on this point differ fundamentally from those of Locy, since according to my determination the line which separates the expanded cephalic plate from the region posterior to it marks the posterior boundary of the auditory invagination. This is of value, in so far as it enables us to distinguish those two regions — which on other grounds have always been held to be distinct — in stages earlier than was formerly possible. The posterior boundary of the cephalic plate is a clearly marked point at a stage before the neural folds begin to be raised dorsally, and it is situated just behind the region of greatest ventral flexure of the cephalic plate (marked by an arrow in Fig. 3, Plate **1**). This point may be traced into later stages, until the neural plate is transformed into a closed tube, when it is seen that it corresponds exactly with the hinder boundary of the hindbrain neuromere numbered VI in my figures (Locy's 10th "neural segment"); opposite this neuromere, as has been stated by many observers, lies in early stages the centre of the auditory invagination. The thickened auditory epithelium extends anterior and posterior to this neuromere; but it is opposite this neuromere that the first invagination to form an enclosed capsule takes place (see Plate **3**, Figs. 15 and 16). In later stages the ear capsule shifts backward, so that its centre comes to lie opposite the hindbrain neuromere numbered VII in my figures, which, as may be inferred from the statement above, lies in — or rather is afterwards differentiated from — the region behind the cephalic plate. I have been able to determine with certainty that the posterior limit of the cephalic plate

---

[1] Locy finds that in later stages segments are added to the occipital region from the region of the trunk (see Tables I. and II.).

is a fixed one from a stage with seven somites, until the plate no longer exists as such. That it corresponds with the posterior boundary of neuromere VI of my figures, I am able to state with equal positiveness. Not having found, as Locy has done, eleven segments in the cephalic plate, by counting which one could determine the limits of the plate, I have been obliged to resort to other means. My method of determination has been as follows. As a fixed point in all the stages examined, I have taken the mesodermal somite marked 7 in Plates **1** to **4**. This, as I determine, is the most anterior somite which becomes innervated by a ventral spinal root; it therefore corresponds, I believe, with van Wijhe's 7th somite.[1] Anterior to this is formed a somite (van Wijhe's 6th), which in early stages possesses embryonic muscle fibres, but never becomes innervated by a motor root. Rabl ('92) said he could affirm with confidence that the somite (Urwirbel) which van Wijhe holds for the 6th or 7th head segment in an embryo with 48 somites is identical with that which he counts as the first trunk segment in an embryo of 76 somites. This mistake [?] of van Wijhe's, the accuracy of whose work in general is so well known, has led me to take especial pains to verify the identity of somite 7 in the stages most carefully examined, viz. from the stage with 6 to 7 somites, until after the neural tube is closed. Its identity has been determined as follows. I have carefully measured the distance from the constriction between van Wijhe's 2d and 3d somites — the mesodermic constriction which appears above the hyomandibular cleft — to the *partial* constriction anterior to van Wijhe's 6th somite. This distance measured in over two hundred embryos by means of camera-projection images, I have found to be practically constant, since it increases only very slightly as the embryo increases in length. Having thus determined the identity of this somite in successive stages, I have had a safe starting point for the determination of the posterior limit of the cephalic plate. I have measured the distance from the posterior cleft of van Wijhe's 7th somite, in the manner described above, to the posterior boundary of the widely expanded cephalic plate, and I have found this distance also to be constant. I chose to measure from the posterior boundary of van Wijhe's 7th somite, because by the measurement of this rather than a less distance the chances of error were diminished. The reader can verify the constancy of this distance by measuring the Figures (3 to 10) on Plates **1**, **2**, and **3**, which were drawn with the aid of a camera, and are magnified forty-three diameters. *This distance is almost precisely the same as the distance from*

---

[1] Van Wijhe's 1e occipital Somit. Rabl's 3e distale Urwirbel.

the posterior boundary of somite 7 to the posterior boundary of neuromere VI, after the closure of the neural tube (see Figs. 7 and 10, Plate **3**, and Fig. 6, Plate **2**), and, as previously stated, the posterior boundary of the auditory invagination at first coincides with the posterior boundary of encephalomere VI. Again, and in direct confirmation of the evidence stated above, the posterior boundary of encephalomere VI is the posterior boundary of a greatly enlarged portion of the neural tube (Figs. 7–10, Plate **3**), as one would naturally expect, if it coincides with the posterior boundary of the previously widely expanded cephalic plate. With this fact in mind it is interesting to compare the conditions I have found with Locy's results. I believe he would not contest the assertion that my encephalomere VI is identical with his neuromere 10 (Zimmermann's encephalomere 11), because its relation to the ear vesicle at the time this is formed makes its identification a simple matter. Locy ('95, p. 522) says of the auditory vesicle: "When first established its centre occupies the space of the segment marked 10. Sometimes, in its earliest stages, the circular area spreads over the space of the three segments marked 9, 10, and 11, but I should say from my observations that, more frequently, it is not so widely expanded. It always settles down in Squalus acanthias to occupy the position first indicated, and subsequently it is shifted backwards." This accords with my identification of his segment 10 with my encephalomere VI, and this conclusion is corroborated by his statement that "the segment marked 8 is seated above a depressed region in which the first visceral cleft appears," for that is precisely the position of the encephalomere IV of my figures. On page 528, however, he says, "When the ear vesicle first arises it makes its appearance opposite the *ninth* neuromere" (!). Again, in his Figures 6 and 9, Plate XXIX., "neural segments," which are described (p. 528) as *8* and *9*, but which I believe to be segments *9* and *10* (as a comparison with my Fig. 46, Plate **7**, shows), are numbered *7* and *8* (!). Here, then, are three conflicts. Despite the elusive nature of Locy's "neural segments," I am disposed to regard his neural segment 10 (opposite which, as he has twice stated, the auditory invagination occurs) as identical in position with encephalomere VI of my figures. If this be true, there is no room on the cephalic plate for his neural segment marked 11, since, according to my determination, encephalomere VII is differentiated from the region of the neural tube which lies *behind* the broad cephalic plate, and does not become clearly marked off from the spinal cord region before a considerably later stage (stage H of Balfour). Therefore, if Locy's neural segment 11 is identical in position with my encephalomere VII, I see no escape from the conclusion that he has not "traced neural segments accurately up to the time they form neuromeres." It is hardly conceivable that he will bring forward in this instance the explanation previously offered in a similar case of mistaken identity, that somehow, between the stage with an open neural plate and a closed tube, segment 10 (neuromere VI) has *insidiously* come to assume the position previously occupied by his segment 11, and that segment 11 has been crowded backward. And it is likewise improbable that he would follow this explanation with another, — as he did in the case mentioned, — that encephalomere VI of my figures represents the "combined vesicle" of his segments marked 10 and 11.[1]

I now turn to the study of what I regard as the true primitive segmentation of the nervous system, — the so called neuromeric segmentation.

II. The "Hindbrain Neuromeres" in S. acanthias.

a. Definition of the Term "Neuromere."

In the preceding description the term "neural segment," or simply "segment," has been used as a non-committal term for structures of such different morphological value as those described by Locy under that name and the regular foldings of the neural tube. Locy ('95) has used the term "metamere" as synonymous apparently with his term "neural segment." Since, however, the term "metamere" is applicable by usage only to the successive similar parts of the body as a whole, it cannot be applied wisely to the successive parts of a single organ system, such as the nervous system.

Ahlborn ('84ᵃ) was the first to use the term "neuromere," and he applied it to all the successive similar segments of the central nervous system. Béraneck ('84) applied the term "replis medullaires" and Kupffer ('86) the term "Medullarfalten" to the regular foldings seen in the brain region of Vertebrate embryos, those of the hindbrain being given by Béraneck the special appellation of "vrais replis." Since the

---

[1] In a paper which comes to hand just as this goes to press, Locy ('97) states that he finds two sets of vesicles in the brain of chick embryos. Of these the first set, numbering seven in all, called by Locy "optic vesicles," are very ephemeral in existence, and have nothing whatsoever to do with the second set, called by him "brain vesicles." In Acanthias (Squalus) also he finds at least nine pairs of "optic vesicles," likewise very transitory. The exact relation of these to the "metameres" or "neuromeres" he does not state.

English equivalent of Kupffer's "Medullarfalten" and of Béraneck's "replis medullaires" (medullary folds) is used with an entirely different meaning from that intended by these writers, Orr ('87, p. 335) employed the term "neuromere" for the folds due to symmetrical constrictions seen in the hindbrain and the thalamencephalon, and distinctly stated that in Lizard embryos no neuromeres are found behind the vagus nerve. This limitation of Ahlborn's term has not, however, been accepted by later investigators. McClure ('89 and '90) again extended the term neuromere so as to include all the constrictions and dilatations of the neural tube, and classified neuromeres into: (1) *myelomeres*, due to constrictions of the myelon; (2) *encephalomeres*, resulting from constrictions of the encephalon. The latter term had, however, been previously used by Wilder ('89) for the large encephalic vesicles. Zimmermann ('91) adopted the term encephalomere, although he did not attempt to compare "Encephalomeren" with "Myelomeren," and Froriep ('94) used the term for theoretically homodynamous segments of the neural tube in the region of the head. He stated that the encephalomeres may correspond with neuromeres, but that this correspondence is not self-evident.

I shall adopt the nomenclature proposed by McClure ('89 and '90). In my account of the segmentation of the brain I shall begin with the conspicuous constrictions and enlargements of the hindbrain, which have uniformly been regarded by morphologists as typical neuromeres or encephalomeres. Orr's ('87) criteria for neuromeres, based on the study of the hindbrain of Lizard embryos, are as follows: (1) "Each neuromere is separated from its neighbors by an external dorso-ventral constriction, and opposite this an internal sharp dorso-ventral ridge, so that each neuromere (i. e. one lateral half of each) appears as a small arc of a circle." (2) "The constrictions are exactly opposite on each side of the brain." (3) "The elongated cells are placed radially to the inner curved surface of the neuromere." (4) "The nuclei are generally nearer the outer surface, and approach the inner surface only toward the apex of the ridge." (5) "On the line between the apex of the internal ridge and the pit of the external depression, the cells of adjoining neuromeres are crowded together, though the cells of one neuromere do not extend into another neuromere." Later investigations have served only to confirm this clear analysis of the structure of a neuromere.

b. DEVELOPMENT OF HINDBRAIN NEUROMERES.

Previous investigators have assumed that the hindbrain neuromeres possess the same characteristics at their first appearance that they do in later stages, whereas it will be shown in Squalus that this is not the case.

The want of abundant material of early stages felt by investigators in most cases is not a hindrance in the case of Squalus, for the early stages are as easily obtained as the later ones. In the study of the development of neuromeres, I have made use, first, of specimens very lightly stained in hæmatoxylin and mounted *in toto* in balsam, and secondly of the usual cross, frontal, and sagittal sections. The series of embryos represented in Plate **3** is chiefly of value in showing the neuromeres in successive stages, and the relations of the masses of cells composing the neural crest, or ganglionic Anlagen (colored blue in the figures), as seen in cleared specimens. The neural tube is represented as seen in optical section, while the other structures of the right half of the embryo are projected upon the median plane.

The earliest evidence of hindbrain neuromeres which I have found is seen in embryos of 14 or 15 somites in which the cephalic plate has not closed in the hindbrain region. In most embryos with that number of somites the plate is already closed, but in cases where it has not, neuromeres IV, V, and VI are seen as thickenings of the lateral walls of the hindbrain before its closure. Usually closure takes place, as in the chick, first in the region of the so called trigeminus Anlage, and later in the region of neuromere V, the most anterior portion of the cephalic plate remaining open as the neuropore until considerably later stages. Figure 7, Plate **3**, shows that in embryos of 14 to 16 somites (in the specimen figured, after the closure of the cephalic plate) four expansions of the neural tube in the hindbrain region are differentiated (neuromeres III, IV, V, VI). The hinder boundary of neuromere VI marks the former posterior boundary of the cephalic plate. The figures show (and this is a point of considerable importance in considering the morphological value of neuromeres) that each neuromere corresponds to the region of a dorsal as well as a ventral expansion of the neural tube, and that the neuromeres are separated from one another by both dorsal and ventral constrictions, which are to be seen both in sagittal sections and in cleared specimens.

Frontal sections at this stage give additional evidence concerning the structure of hindbrain neuromeres. A frontal section just below the axis of the neural tube is shown in Figure 22, Plate **5**. The section shows that the cephalic plate is still open in the region of the forebrain. The dorsal portion of the mesoderm in the region of van Wijhe's 2d and 3d head somites (2 and 3) is cut on the right side only, the sections not being exactly frontal on account of the torsion of the embryo. The lateral walls of the neural tube are seen in the figure to be thickened in that region which lies just posterior to the constriction opposite van Wijhe's 3d somite. A comparison of many frontal and sagittal sections leaves no doubt that this thickening lies in the region of neuromere IV. That expansion of the neural tube which lies between the 2d and 3d somites, and which is separated by an external constriction from neuromere IV behind and from the midbrain vesicle (encephalomere II of my figures) in front, is the most anterior of the primary expansions or encephalomeres of the hindbrain. It has been called by Zimmermann ('91) "Hinterhirn." This corresponds to the third expansion of the neural tube in the chick (Fig. 44, Plate **7**), as may be determined by its relation to the acustico-facialis Anlage and the auditory invagination. Failure correctly to identify this vesicle in the chick led Miss Platt ('89) to call the second vesicle, viz. the primary *midbrain*, the *hindbrain.*

At a later stage, when 17 to 18 somites are differentiated, a well marked local thickening in the posterior half of encephalomere III appears.[1] A frontal section of an embryo at this stage, showing neuromere IV as a local thickening posterior to neuromere III, is seen in Figure 23, Plate **5**. Encephalomere III is separated by a constriction from encephalomere II. At this stage, then, only four of the hindbrain neuromeres (III, IV, V, and VI) are differentiated, and the conditions remain the same when one more somite is formed.

In a similar frontal section of an embryo with 19 somites, such as is represented in Figure 24, four symmetrical thickenings of the lateral walls of the hindbrain (III–VI) appear. Opposite neuromere V lie the cells of the Anlage of the acustico-facialis nerve (blue), and opposite neuromere VI the thickened auditory epithelium. Neuromere VII is not present at this stage, and it does not begin to be differentiated until after one or two more mesodermal somites are formed, when a faintly marked dorsal and ventral dilatation appears in the region of the neural tube just behind neuromere VI (Fig. 9, Plate **3**). The lateral walls of this neuromere never become so markedly thickened as the walls of the other neuromeres, nor does the neuromere show a constriction at its posterior border before the embryo reaches the condition of Balfour's stage H, and then only a faintly discernible one. A cross section through neuromere IV, which serves to show how greatly thickened the lateral wall is at this stage, is shown in Figure 32, Plate **5**. The dorsal wall of this neuromere is considerably thicker than that of the neuromeres anterior and posterior to it, possibly because few cells are proliferated from this neuromere to form the ganglionic Anlage or neural crest.

---

[1] Such a secondary subdivision of encephalomere III. ("Hinterhirn") occurs in the chick as in S. acanthias. I regard the primary vesicle as of different morphological value from that of its subdivisions, for reasons which will be made more apparent when the relations of the vesicles are studied.

I pass now to a description of the hindbrain neuromeres (encephalomeres) at a stage with 28 or 30 somites (Balfour's stage H). Since at this stage the neuromeres are clearly differentiated, and the thinning and expansion of the roof of the hindbrain have progressed very little, this is a most favorable stage for the study of the structural and histological peculiarities of the hindbrain neuromeres.[1] Figure 13, Plate **3**, represents a cleared specimen at this stage, and Figure 25, Plate **5**, a frontal section of the same. Opposite neuromere III (Fig. 25) lies part of the trigeminus Anlage; opposite neuromere V lie the cells of the acustico-facialis Anlage; and opposite neuromere VI lies the thickened auditory epithelium, which is just beginning to invaginate. The acustico-facialis Anlage always remains in relation with neuromere V, so that this serves as an excellent starting point in counting the neuromeres. In order to get a clear conception of the structure of the neuromeres, cross, frontal, and sagittal sections are necessary. The series represented in Figures 36–38, Plate **6**, are frontal sections taken at different levels (α, β, γ, Fig. 40, Plate **6**) in the medullary tube. Only the right wall of the medullary tube in the region of neuromeres IV and V is shown in detail. The first section (Fig. 36) is dorsal, in the region of the "Deckplatte." In this section it is seen that what Orr ('87) has said for the Lizard (see page 167) is true for Squalus. The section reproduced in Figure 37, more ventral than Figure 36, shows that the conditions which obtain in the region of the lateral zones are somewhat different from those of the dorsal zone. Since no sharp internal ridge exists, each lateral half of a neuromere does not appear in section as an arc of a circle, but as a thickening of the wall of the medullary tube. The cells and nuclei are fewer in number and more crowded in the region of constriction between neuromeres. Although there is no inner concavity at this level, the cells and nuclei (Fig. 37) show a radial arrangement similar to that shown in Figure 36. The ventral section (Fig. 38) differs in no essential respect from the dorsal one. I have chosen these two neuromeres (IV and V) for description, since they with neuromere VI show the characteristics stated above in the most marked way. Only a faint external constriction, without internal constriction or ridge, separates neuromere VII from the region of the spinal cord.

---

[1] The head somites, likewise, appear at this stage most clearly differentiated. It is, in fact, the "acranial stage" of the embryo.

At a stage with fifty somites (Balfour's stage K) the structure of the neuromeres is slightly but not materially changed. In Figure 17, Plate **3**, is represented an embryo of this stage, viewed as a transparent object. Figures 26–29, Plate **5**, show four frontal sections of such an embryo, Figure 26 being the most dorsal, and Figure 29 the most ventral of the series. Figure 26 shows that the most dorsal portion of the Deckplatte has become very thin, being only one layer of cells thick. The constrictions and dilatations are only faintly shown, the nuclear arrangement being the same in the region of the constriction as in the region of dilatation. Figure 27, more ventral than Figure 26, though still in the region of the Deckplatte, shows the conditions, both nuclear and cellular, to be almost precisely the same as in Figure 36, Plate **6**. The internal ridges, or cusps, are sharp, and the cells in the region between the internal ridge and external constriction are closely crowded together. It is to be noted that the separation of the lateral walls of the hindbrain is least marked in the region of neuromere VI, opposite which the ear capsule lies (compare Fig. 17, Plate **3**). Figure 28 seems to show that the neural walls have become considerably thickened in the region of the lateral zones. There is no doubt that the lateral zones are absolutely and relatively thicker than at the stage last described, while the neuromeres have increased in length. It is to be observed that this thickening is accompanied by a change in the outline of the lumen of the tube, vertical grooves appearing in the place of the vertical ridges of the more dorsal sections. In the most ventral of the sections, Figure 29, the internal ridges appear again, though the concavity of the inner surface of each neuromere in the antero-posterior direction is only faintly indicated.

During stage K, as the result of the great expansion and thinning of the Deckplatte in the region of the medulla oblongata, the neuromeres come to affect only the lateral zones. Locy ('95, pp. 524 and 525) notes changes in the appearance of the "neural segments" at this stage, the explanation of which he does not state with precision. His opinion seems to be, however, that a union of part of each of the original segments with the segment lying just in front of it, accounts for this condition. An examination of the series of Figures 7 to 21 of my Plates **3** and **4**, and of the frontal sections of Plate **5**, shows that no such fusion of neuromeres takes place. The constrictions and ridges between neuromeres never shift their position, the only change being a gradual assumption, by each of the local thickenings, of an inner concavity in the region of the lateral zones.

Frontal sections of an embryo 15 mm. long show that dorsally all traces of the neuromeres are lost. A frontal section in the region of the lateral zones from an embryo of this stage is represented in Figure 30, Plate **5**. A great separation of the lateral walls of the medulla is seen to have taken place in the region of neuromeres III, IV, and V. At this stage only do the neuromeres possess the characteristics described by Orr for the Lizard (see page 167). While the external constrictions are only faintly shown, owing to the increase of the "white substance" on the sides of the medulla, the internal ridges and concavities are well marked. From this stage onward the neuromeres begin to disappear. In embryos of 40 mm. to 50 mm., neuromere VI, in relation with the facialis nerve, is the most clearly marked of the neuromeres.

Before passing to an examination of the evidence of neuromeres in the trunk region, I wish to emphasize the fact that the hindbrain neuromeres cannot be regarded as structures dependent upon the pressure of mesodermal somites. Being local thickenings of the lateral wall of the neural tube they are obviously inexplicable on such a simple mechanical basis. They are structural differentiations of the tube in regions where the mesoderm has not yet extended, — that is, in the dorsal and lateral portions of the tube, the mesoderm of the head being still ventral in relation to the neural tube.

c. SUMMARY.

In the preceding study of the hindbrain neuromeres in S. acanthias, I have supplemented Orr's criteria (applicable to later stages) by a description of the structure of the neuromeres in Squalus in earlier stages of development, i. e. in embryos of 14–50 somites. The characteristics possessed by hindbrain neuromeres in these earlier stages may be summarized as follows. Each neuromere is separated from its neighbor by an external constriction, which passes entirely around the neural tube. There is dorsally and ventrally an internal ridge corresponding to this external constriction; but the ridge vanishes in the region of the lateral zones, being replaced by an internal depression or groove. The nuclei of the lateral wall are, however, still arranged (Fig. 37) in a manner which approximates that of the region of the internal ridges, notwithstanding that the thickening of the lateral wall of the neuromere has actually obliterated all surface evidence of such a condition. Each hindbrain neuromere, therefore, consists of a lateral thickening and a dorsal and ventral dilatation of the wall of the neural tube. The constrictions are exactly opposite on the two sides of the brain. The elongated cells are placed radially to an imaginary point situated in the middle of the thickening of the wall opposite. The nuclei are generally nearer the outer than the inner surface, and approach the latter only in the region of the constriction between the neuromeres. In this region the cells are more crowded, but the cells of one neuromere do not extend into the adjacent neuromeres.

The hindbrain neuromeres, being structural differentiations of the walls of the neural tube, are not to be explained as the result of a simple mechanical process. The essential similarity of these serial groupings of nerve cells to the metameric ganglia of Annelids will, I believe, impress others as well as myself. A reconstruction of the neuromeres as they appear in this typical condition is shown in Figure 40, Plate **6**.

III. The Neuromeres in the Trunk Region.

a. DEVELOPMENT OF MYELOMERES.

It might seem that a more natural sequence in the study of neuromeres than the one here followed would be to pass from the simpler conditions which obtain in the trunk to the more complicated ones in the head region. Instead of this, I follow the historical sequence, having begun with the "Kräuselungen," or foldings, first seen by observers in the region of the hindbrain, and now pass to the study of the conditions in the spinal cord. That "hindbrain neuromeres" could be compared with segments of the spinal cord was an afterthought on the part of embryologists, evidently born of the conception that the head has a segmentation comparable with that in the trunk.

While the neural plate in the trunk region is still widely open, its dorsal surface exhibits cross furrows, which are proved by longitudinal sections to correspond with the interspaces, or clefts, between the mesodermic somites. The number of the cross furrows exactly equals that of the interspaces, increasing in number as the constrictions between the somites do. They do not, however, extend to the edges of the neural plate, but are restricted to the region where the plate rests upon the somites. In these cross furrows we have the first indications of those structures which were called by McClure ('89) "myelomeres," and were compared by him with the "neuromeres" of the medulla.[1] Such symmetrical cross furrows on the widely expanded neural plate of embryos of Salamandra atra were described by Kupffer ('86), and considered by him as remnants of a primitive segmentation. Since Kupffer believed that at this stage there was no trace of mesodermic somites, he regarded the segments as "primary," i. e. not formed secondarily in adaptation to the mesodermal segmentation. Both Froriep ('92) and Wiedersheim ('92) have, however, declared that mesodermal somites are present at the stage described by Kupffer, and that the segments could be explained as the passive result of the pressure of these somites. Locy ('95) finds in the trunk region of embryos of S. acanthias with a widely expanded cephalic plate that the lines of division between his "neural segments" may be traced inward toward the median furrow, probably as the result of the appearance of somites in that region. As stated on page 160, I have failed to find this exact correspondence between the neural segments of Locy and the somites.

When the neural plate has closed to form the neural tube, the regions of elevation between the furrows become constrictions, which however affect only the ventral half of the tube, i. e. that portion against which the somites lie (see Fig. 41, Plate **6**). Neither frontal sections nor cleared specimens give evidence of constrictions in the dorsal half of the tube. The constrictions in the ventral half of the tube are most clearly marked in the early stages, when the mesodermal somites are most rounded in form, and they disappear as this rounded form disappears.[2]

Figure 39, Plate **6**, represents a frontal section in the ventral half of the myelon of an embryo with 28–30 somites (Balfour's stage H). The right half of the neural tube and of the mesoderm is shown. It is seen that the wall of the neural tube shows a rounded constriction opposite the somite, while opposite the cleft between two somites, and conforming with it, an outer ridge and an inner rather sharp groove are seen. This section affords evidence more favorable to the contention that "neuromeres" exist in the spinal cord than that seen at any other stage of development, or in any other plane of sectioning. In dorsal sections of the same series the constrictions disappear, as do the somites also.

---

[1] Marshall ('78) had previously stated that in the chick "the cord is slightly constricted opposite the centres of the protovertebræ, and slightly dilated opposite the intervals between successive protovertebræ."

[2] Miss Platt ('89) has said with regard to the chick, "Here [in the trunk region] as in the medulla, the segmentation is more manifest in the ventral region than in the dorsal."

The structure of the myelomeres in embryos of 40–50 somites is represented in Figures 42 and 43, Plate **6**. As in Figure 39, only the right half of the embryo is shown. The only evidence of the structural peculiarities of neuromeres at this stage consists in an external constriction opposite the myotome and the spinal ganglion (Fig. 43). In sections dorsal or ventral to the one shown in Figure 43, even this constriction becomes lost (see Fig. 42, which is more ventral, occupying the region of the ventral roots). All traces of an internal dilatation and constriction, and of the concomitant radial arrangement of cells, have disappeared. In the head, on the contrary, the "neuromeres" still preserve all the characteristics seen in the earlier stages.

An examination of the structure of the myelomeres shows that the conditions are easily explicable on the mechanical grounds stated. There are no serial thickenings of the wall of the neural tube, as in the hindbrain, and the radial arrangement of cells and nuclei shown in the frontal sections (Fig. 39) presents no difficulty; for the cells composing the epithelium of the neural tube always have their long axes perpendicular to the surface of the tube, so that, if the tube becomes constricted opposite each somite, the cells will necessarily show a radial arrangement in frontal sections. In view of this fact, it is difficult to understand how investigators should have thought that the existence of a radial arrangement of cells and nuclei was evidence sufficient to establish the morphological value of myelomeres, and their serial homology with hindbrain neuromeres. McClure ('90), for example, says, "The lateral walls of the spinal cord are divided into neuromeres which, while less conspicuous, have all the cellular characteristics seen in the typical neuromeres of the hindbrain, and in fact are a continuation of the latter." That all of the cellular characteristics seen in the typical neuromeres of the hindbrain are also found in the myelomeres is demonstrably untrue for Squalus, as may be seen by comparing the sections shown in Figures 38 and 39, Plate **6**, both from the ventral half of the neural tube of the same embryo, one in the head and the other in the trunk. The cellular arrangements are decidedly unlike. In the head (Fig. 38) the cells and nuclei are crowded in the region of constriction between neuromeres, while in the trunk, if the cells are crowded at all, it is in the region of dilatation of the myelomere.

It has seemed a strong argument for the serial homology of myelomeres and hindbrain neuromeres that the former continue into the latter gradually and in an unbroken series. For example, McClure ('90) stated that "the constrictions of the myelon (in Lizard embryos) gradually pass or merge into those of the encephalon, thereby forming a continuous series of constrictions throughout the entire length of the neuron, which increase in size anteriorly." Also, in demonstrations of this continuity, Miss Platt ('89) stated (for the chick) that "the difference (in size) between the fifth neuromere [last neuromere of the medulla] and the next posterior fold is not as great as the difference between the second and third neuromeres." (Compare Fig. 44, Plate **7**.) Locy ('94 and '95) says of his neural segments that "those in the trunk region are continuous with those of the head, and pass into the latter without any transition forms." Zimmermann ('91), on the other hand, does not find the spinal cord in S. acanthias to be segmented.

While I am able to confirm the evidence of continuity of encephalomeres and myelomeres as stated by previous investigators, I am unwilling on this ground alone to regard these structures as of the same morphological value. Moreover, it has been shown that the hindbrain neuromeres and the myelomeres differ both in structure and in development.

b. SUMMARY.

The evidence presented by the constrictions of the myelon warrants the inference that the existence of the myelomeres is dependent upon the presence of the somites, an explanation by no means possible for the hindbrain neuromeres. The constrictions of the myelon appear only after the somites are formed, and increase in number with the addition of new somites. They are opposite the somites, and are confined to that portion of the neural tube against which the somites lie, i. e. the ventral portion. They present no histological or structural conditions which are not easily reconcilable with the hypothesis of their mechanical formation. In those Vertebrates in which the somites extend farther dorsally with reference to the neural tube, the constrictions of the myelon also have a greater dorsal extent. As soon as the somites lose their rounded form and no longer lie close to the neural tube, the constrictions of the tube disappear. As a whole, the evidence in the spinal region of Squalus fully confirms the explanation given by Minot ('92), viz. that the appearance of the myelomeric constrictions "seems to depend upon the development of the primitive segments of the mesothelium. When the segments are fully formed, and before their inner wall has changed into mesenchymal tissue, they press against the medullary tube and oppose its enlargement; at least one sees that the tube becomes slightly constricted between each pair of segments and slightly enlarged opposite each intersegmental space." Structurally, therefore, myelomeres and encephalomeres differ. While a mechanical explanation is possible for the one, such is not possible for the other. They are, it is true, continuous serial dilatations of the neural tube. The proof, however, that they are of equal morphological value, that is to say, serially homologous, rests, I believe, in the demonstration of a similar metameric relation to organs known to be segmental. The myelomeres correspond metamerically with the somites, as has been stated. Do the encephalomeres likewise correspond with somites? Upon the answer to this question obviously depends largely the decision as to their *metameric* value. Before stating the evidence bearing upon this question it is necessary to see if there is any evidence of neuromeres anterior to the hindbrain.

IV. The Neuromeres anterior to the Hindbrain.

a. ESSENTIAL CRITERIA OF NEUROMERES.

I believe that those who find neuromeres in the brain region anterior to the hindbrain have assumed the presence of a homodynamous segmentation of the entire encephalon. Yet it must be admitted that even if a serially homologous segmentation extends from the spinal cord into the medulla oblongata, it by no means follows that such segmentation also extends into the anterior brain region. Compare with the analogous case of the skull. Because the occipital region is segmental, i. e. composed of fused vertebræ, it does not follow that the pre-otic region is. It is well, at least, to study the conditions in the anterior brain region with the mind as unprejudiced by any theory as possible. What criteria, then, warrant the conclusion that any given division of the neural tube is a neuromere? Certainly, no one criterion would be held to be sufficient. The best criteria are such as associate the supposed neuromeres metamerically with other structures known to be segmental, e. g. the mesodermic somites or the segmental nerves. But where such direct evidence is wanting, to say that a radial arrangement of cells and nuclei is evidence of a neuromere, and thus indirectly evidence of a metamere, is obviously dangerous, since the radial arrangement of the nuclei appears whenever the neural tube is constricted from any cause whatever.

If, however, we have rudimentary somites in the head, may we not also have rudimentary neuromeres? McClure ('89) finds between the midbrain and the optic vesicle of the Lizard a structure which resembles a portion of a neuromere, — a "half-neuromere." He accepts the evidence of neuromeres in the primary forebrain also, although the arrangement of nuclei does not always conform to the typical condition. Waters ('91, p. 143) says: "In this area [that of the posterior commissure] the Cod brain shows little or no segmentation, but from the fact that it nearly corresponds in extent to neuromere II, and that its existence is quite evident in Amblystoma, it seems probable that this space is occupied by the third and last of the forebrain neuromeres." In other words, though none of the characteristics of a neuromere are present, it is *a priori* probable that a neuromere exists here!

Orr, Béraneck, and Miss Platt have regarded the midbrain vesicle as a single enlarged neuromere. It has an external constriction separating it from its neighbours, a corresponding internal ridge, an inner concavity, an outer convexity, a radial arrangement of cells and nuclei, and in addition is primary in time of appearance. On the other hand, Waters ('92) says that it is an error to confound the neuromeric segmentation with the so called vesicular segmentation, since he finds in the midbrain region "*two*[1] well marked convolutions of the brain wall," and the characteristic radial arrangement of nuclei. Kupffer ('93^a) believes that, since, with Froriep (92^a) and Zimmermann (91), he finds evidence of *three* encephalomeres in the midbrain,[2] this confirmation gives a certainty to their results.

Surely the divergence in the results of other investigators has not *proved* that Orr, Béraneck, and Miss Platt were wrong in considering the primary midbrain as a single neuromere, especially since the midbrain and forebrain form parts of a continuous series of primary enlargements of the encephalon. The majority of investigators (Orr, Béraneck, McClure, Froriep, and Zimmermann) find that the forebrain consists of *two* neuromeres, without however giving a satisfactory explanation of its marked divergence, in the matter of secondary division, from the typical hindbrain dilatations. If we count dorsal expansions, as is done by Waters and others, we may find evidence of at least *three* neuromeres, which correspond, says Kupffer ('93^a), with his Grosshirn, Nebenhirn, and Schalthirn. Furthermore, if dorsal diverticula be regarded as evidence of neuromeres, we must agree with Kupffer that it is impossible to disregard the epiphyses and plexus formations.[3] On this basis

---

[1] Waters says (p. 465) that he thinks McClure is mistaken in assigning to the midbrain region, on purely speculative grounds, a *third* neuromere.

[2] Kupffer found these three secondary subdivisions of the midbrain in Cyclostomes, Zimmermann in Selachii, and Froriep in Mammalia.

[3] See Kupffer ('93^a, p. 549).

Kupffer finds at least *five* encephalomeres in the primary forebrain. This conclusion seems strengthened by the conclusion of Burckhardt ('93), that the median zones of the neural tube retain throughout the Vertebrate series the primitive segmentation best, and therefore are the best for comparison.

My conclusions from a study of the evidence presented by those who have assumed a segmental value for the secondary subdivisions of the forebrain and midbrain vesicles are, (1) that morphologically different structures have been described by them as "neuromeres" or "encephalomeres," and (2) that the divergence in their results does not seem to justify this assumption.

I now turn to an examination of the development of forebrain and midbrain regions in S. acanthias, in order to determine whether or not it is probable that structures morphologically comparable with hindbrain neuromeres exist in these regions. Since hindbrain neuromeres involve all three zones — dorsal, ventral, and lateral — of the walls of the encephalon, the value of forebrain and midbrain segments as morphological equivalents of them will clearly depend on their similarly involving those zones. If they do not, it is incumbent upon one who holds to their equivalency to demonstrate how modification has probably obscured or obliterated the primitive conditions. Evidence in such a highly specialized region can be at best only probable. Here, however, as always, the demonstration of morphological comparability must be "controlled" by the demonstration of similar relationships to other organ systems.

b. DEVELOPMENT OF THE FOREBRAIN AND MIDBRAIN.

At a stage with 19 or 20 somites the conditions in the anterior brain region are very simple. The primary forebrain and midbrain are simple vesicles or enlargements of the neural tube. A parasagittal section cut through the right wall of the neural tube is represented in Figure 45, Plate **7**. Six vesicles are counted, all of them being included in the region of the cephalic plate. The anterior vesicle shown is the wall of the forebrain in the region of the optic vesicles. Behind lies the midbrain, separated by a slight constriction from that region of the hindbrain to which Zimmermann ('91) has given the name "Hinterhirn."[1] Hindbrain neuromeres IV, V, and VI are clearly defined.

A frontal section of an embryo of the same stage, so cut as to coincide with the axis of the midbrain vesicle, is shown in Figure 49, Plate **7**. The vesicle of the primary forebrain (I) appears as an almost circular enlargement of the anterior portion of the neural tube. Behind this, and separated from it by a constriction, lies the narrower and somewhat more elongated midbrain vesicle (II). Posteriorly a small portion of the "Hinterhirn" vesicle also appears in the section.

---

[1] The English term hindbrain has been applied to the region separated by the Germans into "Hinterhirn" and "Nachhirn."

Sagittal sections of embryos at this stage are seen in Figures 8 and 9, Plate **3**. Faint dorsal constrictions separate forebrain, midbrain, and "Hinterhirn" (III), the separation between midbrain and "Hinterhirn" being very slight. A deep depression in the floor of the forebrain marks the position of the infundibulum, which is bounded posteriorly by a faint constriction, the first indication of the tuberculum posterius (Kupffer). Another constriction of the ventral wall of the neural tube is seen behind the tuberculum posterius in the region of the midbrain, — the plica encephali ventralis. In later stages the region of this constriction becomes the point of greatest flexure of the neural tube. The constrictions marking off the brain vesicles appear as rather broad depressions, not sharply defined as are the constrictions between neuromeres. The brain vesicles are also seen to be considerably larger than the hindbrain neuromeres, the difference in size constantly increasing from this stage onwards. Except for a local thickening of the lateral zones, the two anterior brain vesicles are structurally quite comparable with the hindbrain neuromeres. They similarly involve all three zones of the neural tube.

An examination of embryos at a stage with 28 to 30 somites, i. e. early in Balfour's stage H, shows that slight changes have occurred. A parasagittal section of such an embryo is shown in Figure 46, Plate **7**. The anterior vesicle, the forebrain, is so cut that one sees its lumen. Behind this, and separated from it by a constriction which extends to the ventral portion of the tube, lies the midbrain, which dorsally is a single expansion passing almost without constriction into the hindbrain. The depth of the constriction is much less than it appears to be in this figure, because the section passes to one side of the median plane. In the ventral half of the midbrain there is a constriction, which more median sections of this stage (Fig. 13, Plate **3**) show to correspond with the region of sharpest flexure of the neural tube (plica encephali ventralis). This constriction does not extend, however, to the dorsal portion of the neural tube, and therefore is not equivalent to a constriction which separates neuromeres. By it the midbrain is separated ventrally into two lateral expansions on each side of the head, — one anterior, the other posterior, — while dorsally it remains a single dilatation. The anterior of the two expansions narrows as it extends ventrally, and terminates at a point in the ventral wall near, but anterior to, the tuberculum posterius. The posterior of the two midbrain expansions is bounded behind by the faint lateral constriction between midbrain and hindbrain vesicles.

The conditions shown in a sagittal section at this stage are not essentially different from those presented at the stage previously described (Fig. 13, Plate **3**). The forebrain, midbrain, and "Hinterhirn" vesicles are separated by very faint dorsal constrictions. In the constriction between forebrain and midbrain vesicles appears later Miss Platt's "thalamic nerve." Ventrally two constrictions are seen, one corresponding with the tuberculum posterius, and the other, more posterior, with the point of greatest flexure of the neural tube. Two frontal sections of an embryo at this stage are shown in Plate **7**, Figures 48 and 50. Figure 48 represents the more dorsal of the two, and shows only the expansion of forebrain and midbrain vesicles separated by the primary constrictions spoken of above. A small portion of the "Hinterhirn" is shown. The section shown in Figure 50 is more ventral, being in a plane about midway between the dorsal and ventral sides of the neural tube. An arrow is drawn at the constriction separating forebrain and midbrain vesicles. This constriction corresponds with the one seen in the more dorsal section, also indicated by an arrow. Behind this, in the region of the midbrain, another constriction appears, one which was not seen in the dorsal section. This may be traced in more ventral sections into the constriction previously described as occupying the floor of the midbrain at a point corresponding with the point of greatest flexure of the neural tube. In my opinion everything in front of the arrow belongs to the primary forebrain, the lateral walls of which are expanded to form the optic vesicles. Behind these two vesicles are seen "two well marked constrictions and two convolutions" of the neural wall which show radially arranged nuclei.[1] It is found in later stages that the posterior of the two constrictions corresponds in position with the posterior commissure, and therefore that what lies anterior to this constriction must be considered as part of the thalamencephalon. It is seen, therefore, that the constriction between primary forebrain and midbrain vesicles does *not* correspond with the posterior commissure, which in later stages forms by common consent the anterior boundary of the midbrain (see

---

[1] Probably the two "neuromeres" of the thalamencephalon described by Orr ('87).

Plate **7**, Fig. 47, *coms. p.*). This constriction corresponds, instead, with a point just behind the epiphysis, and is separated from the posterior commissure by that portion of the brain which Kupffer has named Schalthirn, or diencephalon (the Schaltstück of Burckhardt). Neither of the so called neuromeres (Orr) is in relation with a nerve, motor, or sensor, and neither possesses a dorsal expansion of its own.

A parasagittal section of the next older stage represented is seen in Figure 47, Plate **7** (compare Fig. 19, Plate **4**); it is of an embryo with 65 somites (Balfour's stage K), and the changes in the anterior brain region are seen to be considerable. In the dorsal portion of the region called primary forebrain, i. e. the region anterior to the constriction in which the "thalamic nerve" (*thl.*, Fig. 18, Plate **4**) lies, two expansions now appear. These are median, unpaired, and separated from each other by a constriction which extends toward, but does not reach, the optic stalk. The anterior expansion is the prosencephalon (Grosshirn, epencephalon of Kupffer), which involves, as determined by His (88^b), the "Deckplatte" and both "Flügelplatten." The second, which at this stage is a simple expansion, later becomes differentiated into "Zirbelpolster" (Kupffer's parencephalon, Nebenhirn) and the epiphysis. The latter, according to His, is derived from the "Deckplatte" only. The primary constriction between forebrain and midbrain is marked in Figure 47 by the dorso-ventral line, behind the second expansion. The midbrain now shows three lateral expansions. The anterior is bounded in front by the primary constriction between forebrain and midbrain, and behind, as in the previous stage, by the ventral (and now lateral) constriction which extends dorsad toward the posterior commissure from a point just in front of the chief root of the oculomotor nerve. The second dilatation has as its posterior boundary a ventral constriction which I do not consider of morphological importance, because it simply corresponds with a point of flexure of the ventral wall of the tube, never extends to a dorsal position, and has no corresponding inner ridge. The constriction exists, however, at this stage, and forms the posterior boundary of a neural segment related to the oculomotor nerve. Behind this lies a third expansion, faintly marked anteriorly and also posteriorly, where it merges into the isthmus. In later stages the trochlear nerve arises from the region of the posterior constriction of this expansion; it is the chiasma of fibres of this nerve which defines the posterior constriction of the midbrain vesicle. In this stage, as in the preceding, the midbrain vesicle remains dorsally a simple expansion, the constrictions affecting only its lateral and ventral walls.

Two frontal sections of an embryo at this stage are seen in Figures 51 and 52, Plate **7**. Anteriorly in the more dorsal section (Fig. 51) is seen the expansion of the prosencephalon. Behind this lies an expansion which might be considered as a neuromere, if a radial arrangement of nuclei and a constriction of the brain wall were alone considered sufficient criteria for such a structure. Since, however, it is simply a dorsal expansion, which is unrelated to nerves, and soon becomes differentiated into adult organs, I am unable to regard it as a neuromere. From it are differentiated "Zirbelpolster" (parencephalon, Nebenhirn, or Zwischenhirnblase) and epiphysis. Posterior to the constriction marked by the arrow, which corresponds with the point so marked in Figure 50, is situated a long expanded portion of the encephalon which passes without constriction into the midbrain vesicle. In the more ventral section (Fig. 52), however, there is seen in this region a constriction which may be traced ventrally to that point from which the anterior root of the oculomotor arises. Two neuromere-like expansions, separated by the constriction between primary forebrain and midbrain, are seen in this stage as in the previous stage described.

Passing now to a much later stage (21–22 mm.), we find (Plate **4**, Fig. 21) that the posterior commissure has come to lie much nearer the base of the stalk of the epiphysis, and thus that the portion of the dorsal wall which is called by Kupffer diencephalon has become much reduced in the region of the midbrain vesicle. Thus it has come about that frontal sections in a plane midway between the dorsal and the ventral walls of the neural tube (Fig. 53, Plate **7**) show only a single neuromere-like expansion. In more dorsal as well as more ventral sections this undergoes constriction, so that it is by no means a simple neuromeric enlargement. A median sagittal section, such as that shown in Figure 21 (Plate **4**), is the most satisfactory for the study of segmentation at this stage. The primary forebrain is now differentiated into the successive dorsal dilatations epencephalon, paraphysis (parencephalon), and epiphysis. Dorsally the midbrain still continues to be a simple expansion, while ventrally traces of the three segments still remain, the anterior one having become much reduced in length.

With the exception of Locy, Zimmermann ('91) is the only investigator who has studied the "neuromeres" in Selachii. For the purpose of comparison, it is well to state his results here. He finds at first *eight* "primäre Abschnitte" in the encephalon, the first three of which exceed in size the last five. The first three are the Vorderhirn, Mittelhirn, and Hinterhirn each of which he regards as a complex of encephalomeres, since they later subdivide into segments which dorsally are equally long and broad. The Vorderhirn divides into two encephalomeres, the Mittelhirn into three, and the Hinterhirn into three. Thus, since the posterior five "primäre Abschnitte" do not further subdivide there are in all thirteen "encephalomeres." As a result of cephalic flexure some of the encephalomeres become wedge-shaped, but all are clearly separated from one another by constrictions. Zimmermann's paper was a preliminary one without figures, and it has not as yet been followed by a final paper.

It is seen that Zimmermann's account, based on the study of S. acanthias embryos, differs somewhat from my own. At the closure of the neural tube I find six vesicles or expansions of the encephalon. The first three correspond with those called by Zimmermann Vorderhirn, Mittelhirn, and Hinterhirn; the last three are hindbrain neuromeres IV, V, and VI. Since Zimmermann's 7th and 8th "primäre Abschnitte" are not differentiated at this stage, I am unable to accept his conclusion that there are at first *eight* primary "encephalomeres" or "Abschnitte." The primary forebrain subdivides into the two dorsal expansions which Zimmermann calls "Secundäre Vorderhirn" and "Zwischenhirn." But, if these are "encephalomeres," I am unable to see how later differentiations, such as the prosencephalon (epencephalon), paraphysis (parencephalon), and epiphysis can be excluded from the same category. May we not have tertiary as well secondary "encephalomeres"? I am unable to accept Zimmermann's single criterion of size as sufficient to enable us to make a distinction between those segments which are primitive, i. e. remnants of ancestral structures, and those which are the early beginning of adult organs. A most serious objection to regarding such structures as Zimmermann's "Secundäre Vorderhirn" and "Zwischenhirn" morphologically comparable with neuromeres or myelomeres has been stated by Herrick ('92), and consists in the difficulty of homologizing dorsal expansions with ventral ones.

The primary midbrain, as stated by Zimmermann, subdivides into three segments, the most anterior of which lies in front of the posterior commissure and in front of the place of origin of the oculomotor nerve. In all stages the midbrain is seen in median sagittal sections to present a simple dorsal expansion, its constrictions affecting its ventral and lateral walls only.

The third vesicle, Zimmermann's Hinterhirn, which he says subdivides into three "Encephalomeren," I find to become differentiated into the cerebellum Anlage and a posterior enlargement or thickening, but nothing more. The only evidence which I find of Zimmermann's anterior "Hinterhirn Encephalomer" consists of a flexure of the median ventral wall appearing in late stages in the anterior portion of the Hinterhirn. Since no dorsal or lateral constriction corresponds with this, and since therefore it cannot be regarded as a vesiculation of the neural tube, I do not consider it as of morphological importance, but explicable simply as a passive result of the flexure of the neural tube.

Locy ('95, p. 542) finds five "neural segments" in the forebrain and midbrain, — three in the former and two in the latter. He clearly figures and mentions in the description of plates, however, the three secondary midbrain expansions described by Zimmermann and myself.

c. SUMMARY.

An examination of the literature bearing on the question of neuromeres in the region anterior to the hindbrain had led me to the conclusion that structures of different morphological value had been described as neuromeres, and the examination of the secondary subdivisions of the forebrain and midbrain of embryos of S. acanthias has served to strengthen this opinion. These subdivisions have been shown to differ from the typical neuromeres in shape, in structure, and in relation to the dorsal and ventral zones of the neural tube. The attempt to establish a serial homology on the basis of such structures alone seems to me quite misleading; not less so, indeed, when we attach hypothetical nerves (dorsal, lateral, and ventral roots) to them.

Moreover, the late appearance of the so called neuromeres of the anterior brain region, together with the fact that they are secondary subdivisions of primary vesicles, and thus differ from the hindbrain and spinal expansions, seems a serious objection to the contention that they afford satisfactory evidence of a primitive metamerism. Zimmermann ('91) attempted no explanation of this difficulty, saying merely that the differentiation of the anterior encephalomeres *is retarded* for reasons unknown to him. Waters ('92) alone offers an explanation. To him it seemed "not unreasonable to conjecture that these constrictions, being essentially primitive and in a state of degeneration, have gradually been more and more crowded out by the specializing brain development, and hence appear at a much later period in the ontogeny than would be expected." What right, we are tempted to ask, has one to *assume* the primitive nature of "forebrain neuromeres," in view of the *facts* that they are late differentiations, and that some of them are the fundaments of adult organs, and in this respect differ both from the typical hindbrain neuromeres and from the expansions of the myelon? Every fact which we possess seems to me to argue against their primitive nature. In my opinion the assumption of Herrick ('92), that, "if neuromeres once existed in the forebrain, they would be visible only at an early stage, and would be obscured by altered conditions," is the more reasonable of the two assumptions. On the basis of structure and of relation to other segmentally arranged organs, however, I conclude that the primary vesicles, the forebrain and midbrain, give evidence — as do the primary expansions of the hindbrain — of the primitive segmentation of the Vertebrate head. I now turn to an examination of these relations, first, to those of neuromeres and somites, since they are the most important.

V. The Relation of Neuromeres to Somites.

a. Relation of Myelomeres to Somites.

Since the myelomeres, as has been stated, show a definite (numerical) correspondence with the trunk somites, the expansions of the spinal cord alternating with the somites, it is evident that proof of the serial homology of myelomeres and encephalomeres will rest very largely on the demonstration of a similar correspondence of the latter with head somites, if there be such. Yet, so far as I know, Miss Platt is the only investigator who has affirmed that there is such correspondence for the head region. She writes ('91, p. 82) as follows: "The line of somites [in Squalus] alternating with the neuromeres is continued into the head as far forwards as the alimentary pocket which is to form the second visceral cleft. Here complete divisions of the mesoderm cease, but serial depressions in its dorsal wall indicate incomplete divisions into three parts above the hyoid arch (van Wijhe found *two* somites here) and two parts above the mandibular arch [van Wijhe found *one* somite here]. Like the somites of the trunk, the divisions thus marked off alternate with the neuromeres, lying opposite successive constrictions of the brain. The anterior division of the mandibular cavity corresponds to the constriction that separates the midbrain from the hindbrain, or to that from which the trochlear nerve arises." The same investigator likewise says in regard to Necturus ('94, pp. 960, 961): "Hinter der Hyomandibularspalte wechseln die primitiven Neural- und Mesoderm-Segmente regelmässig mit einander ab. Die mesentodermale Segmentation ist dieselbe, die von v. Wijhe den Selachiern zugeschrieben wird."[1]

---

[1] It is seen that Miss Platt finds the segmentation, both neuromeric and mesomeric, different in Squalus and Necturus. While in embryos of the former she

b. Relation of Encephalomeres to Somites.

With Hoffmann ('94 and '96) I am able to confirm the presence of van Wijhe's head somites in Squalus (Acanthias) and also Platt's "anterior" somite. Valuable as this repeated confirmation appears to me, I regard as equally important the fact that anterior to the sixth (van Wijhe's) somite *a mesodermal segment corresponds to each of the primary encephalic vesicles* (encephalomeres I to VII). A topographic alternation, however, such as that affirmed by Miss Platt for the hindbrain region of Squalus and Necturus, I do not find. In the early stages of development van Wijhe's sixth somite lies opposite the posterior constriction of encephalomere VII, but this relation is soon lost. However, the numerical correspondence seems important, and I believe that it will be shown by a study of nerve relations that the correspondence is not without morphological significance.

c. Somatic Value of the Pre-otic Mesoderm Segments.

Although it has been stated that the purpose of this paper is to discuss the nature of the neuromeric segmentation and the relations of neuromeres to other segmental structures, it seems to me not inconsistent with this purpose to inquire into the credentials of those mesodermal segments in the Selachian head which van Wijhe in his famous paper considered of somatic value. The confirmation of their presence in Squalus given by Hoffmann ('94 and '96) and myself ('96), while strengthening the belief in their permanency, which has been greatly shaken by the discovery of more numerous segments in other Selachii (Torpedo), by no means demonstrates their somatic value.[2] The dis-

---

finds in the hindbrain region two more somites than were seen by van Wijhe ('82) and a numerical correspondence of these with the neuromeres, in the latter, on the contrary, she finds neuromeres corresponding with a somatic segmentation which is the same as that found by van Wijhe. She finds, therefore, it may be inferred, two less hindbrain neuromeres in Necturus than in Squalus. In embryos of Amblystoma I find, in agreement with McClure ('90), no neuromere corresponding with encephalomere IV of Squalus, i. e. there is one less neuromere in the Urodele than in the Selachian. Now, since I find a numerical correspondence of van Wijhe's somites with hindbrain neuromeres (encephalomeres III–VII) in the Selachian, it is clear that they could not likewise correspond in the Urodele. However, I have been unable to find evidence of pre-otic somites in Amblystoma, and therefore am unable to affirm or deny a correspondence of neuromeric and mesomeric segmentation in this form.

[2] It is a matter of great interest that the latest investigation upon Torpedo (Sewertzoff, '98) shows that the mesodermic segmentation in Torpedo and Pristiurus is the same. Thus van Wijhe's results receive repeated confirmation.

crepancy in the results of investigators of the mesomeric, as well as of the neuromeric, segmentation most certainly justifies Rabl's ('89) complaint of the hasty way in which investigators have given mesodermal segments somatic value. In no question of morphology to-day is conservative judgment more needed. Before stating my own evidence I will briefly summarize the arguments advanced by previous investigators for and against the somatic value of the mesodermal segments of the head.

(1) In addition to the evidence first stated by Marshall ('81), that the dorsal mesoderm of the head of Selachian embryos undergoes a segmentation independent of the segmentation of the visceral arches, van Wijhe ('82, p. 4) uses the following arguments for the somatic value of his somites : "(2) Dass die Länge der Somite sich im ganzen Körper gleich verhält. (3) Dass die obere Grenzlinie der Rumpfsomite ununterbrochen in diejenige der Kopfsomite übergeht. (4) Dass die untere Grenze der Somite sowohl im Kopfe als im Rumpfe nur wenig unter der oberen Grenze des Darmes liegt." The latter proof has been amplified by Killian ('91) from the evidence that the head somites are dorsal in relation to chorda, dorsal aorta, and epibranchial (medio-lateral) line. (5) Hoffmann ('94) and Miss Platt ('97) have confirmed van Wijhe's statement that the development of the somites begins in the neck region and proceeds continuously both posteriorly and anteriorly. Furthermore (6) the same constituent parts, viz. myotome and sclerotome, may be distinguished in the head as well as in the trunk somites (van Wijhe, '82, Killian, '91). To this Miss Platt ('91) adds (7) the evidence that, as in the case of the somatic musculature of the trunk, the muscles derived from the "anterior," the first, the second, and the third somites (rudimentary in the case of the anterior and somewhat modified in the case of the first somite) first appear in the median wall of these somites. Finally (8) there is a correspondence of the neuromeres and mesodermic segments throughout the entire length of the neural tube (Neal, '96).

The following are the arguments advanced in opposition to the somatic value of the mesodermal segments of the head.

(1) The divisions of the mesoderm of the head are due to the mechanical influence of the neighboring parts, chiefly that of the visceral pouches (Kastschenko, '88).

(2) The divisions are irregular in size (Kastschenko, '88, Rabl, '89).

(3) In van Wijhe's third proof there is "nicht die Spur eines Beweises für die Richtigkeit seiner Ansicht" (Rabl, '89, p. 234).

(4) The 1st somite is an exception to van Wijhe's fourth argument (Rabl, '89) ; moreover, the constrictions are never complete in the case

of the somites 2 to 5 (Katschenko, '88, Rabl, '89), so that it is impossible to state the position of their lower boundary with reference to the dorsal wall of the alimentary canal (Rabl, '89).

(5) The development of the "head cavities" is discontinuous with that of the trunk somites (Rabl, '89, Kupffer, '93). While the development of the pre-otic segments takes place later than that of the trunk somites, the differentiation of mesenchyma takes place much earlier in the head than in the trunk. This conflicts with the law, that in the Anlagen of serially homologous organs the older the Anlage the earlier the histological differentiation (Rabl, '89).

(6) There never appears in the case of the pre-otic segments a differentiation into myotome and sclerotome (Rabl, '89, p. 235).

(7) While the musculature of the trunk and occipital somites arises exclusively from the median wall of the somite, the musculature of the pre-otic segments has its origin in greater part from the lateral, and in smaller part from the posterior wall of the so called somites.[1] Moreover, while only a distinct and sharply defined portion of the trunk somites proliferates mesenchyma, the entire median wall of the pre-otic segments participates in the formation of mesenchyma (Rabl, '89).

(8) The topographic relations of the dorsal nerves in later stages are different in head and trunk. In the head the nerves grow laterad to the somites, while in the trunk they grow mediad to them (Rabl, '89).

Special arguments, in addition to the general ones stated above, concerning the nature of the anterior, the 1st, and the 2d mesoderm segments have been made, because of their marked peculiarities in development, structure, and relations, and of their important bearing upon the question of the morphology of the eye muscles. It will therefore be necessary to state these also.

Two chief opinions concerning the nature of the anterior (Platt's) and the 1st and 2d (van Wijhe's) mesoderm segments are now held: (1) that they are serially homologous with trunk somites (van Wijhe, Platt, Hoffmann, Neal, Fürbringer); (2) that they are abortive visceral pouches (Kupffer, '88, Froriep, '92, Sewertzoff, '95). The discussion, therefore, turns upon the question whether these structures represent diverticula (dorsal) of the mesoderm, or lateral diverticula from the alimentary canal.

Miss Platt ('91, '91^a) argues for the somatic value of the anterior somite (cavity) as follows: — (1) In position, independence, and time of origin this cavity resembles the following ones. (2) Many cells from its median wall migrate into the centre of the cavity, and cells bounding the inner wall above and below assume the elongated contour of muscle cells.

---

[1] Balfour ('81) holds that both median and lateral walls of the trunk somites form the lateral trunk musculature.

Hoffmann ('94, p. 649) also, while not able to state with definiteness that the anterior cavity is a dorsal or lateral diverticulum from the alimentary canal, i. e. whether it represent a mesoderm segment or a visceral pouch, considers it probable that it represents the former, since it is very similar to the succeeding head cavities of van Wijhe. Hoffmann mentions the migration of cells into the cavity of the somite, but does not specify from which wall they are proliferated. He also states that from the walls of the somite "entstehen keine Muskelfasern" ('96, p. 256). Against these views of Miss Platt and Hoffmann no special arguments have as yet been raised.

The first somite of van Wijhe possesses the peculiarity of a median stalk connecting the somites of the opposite sides of the body.[1] The relations of this stalk to the dorsal wall of the alimentary canal, to chorda, and to dorsal aorta have been used as the chief criteria in contending for its dorsal or its ventral nature. The evidences that the first somite represents somatic (dorsal) mesoderm are as follows: (1) Its cells are proliferated from the dorsal wall of the alimentary canal (Platt, '91^{a}).[2]

---

[1] Such a median connection, however, also appears in the early stages of development of the "anterior cavities." The connecting stalk of the "anterior cavities," however, as stated by Hoffmann, never possesses a lumen, as does the median connecting stalk of the premandibular cavities.

[2] Miss Platt, in her earlier paper ('91, p. 81), states that the mesoderm of the premandibular cavity is formed, at least in part, by a proliferation of cells from the mandibular cavity, while in her later paper ('91^{a}, p. 256) she writes, "The most anterior mesoderm of the head does not take its origin from the mesodermic plates, but from the dorsal wall of the alimentary canal. The mesodermic plates end with the mandibular cavities." The lumen of the connecting stalk, according to Miss Platt, is, as stated by Marshall ('81), formed secondarily by the fusion of a median with the two lateral cavities. This evidence is interesting, since it bears on the question whether the cavity of the connecting stalk is to be regarded as a part of the archenteron, and would seem to answer this question in the negative. Killian ('91, p. 102), however, finds the connecting stalk a "Sklerotomkommissur," and thus, it is to be inferred, the lumen of the stalk, which according to his account is formed secondarily, not a part of the archenteron. He states (p. 102): "Erwähnt sei noch, dass zwischen den beiden ersten Mandibularsomiten vor dem vorderen Chordaende und über dem Aortensinus ein Mesodermzellenhaufen liegt, der die Sklerotomanteile beides Somiten in Verbindung setzt (Sklerotomkommissur). Was nun der Oralzone angeht, so entsteht sie dadurch, dass die vordersten Zipfel des ursprünglich schwalbenschwanzförmig endenden dorsalen Mesoderms die vordere Darmkuppe (vordere Ektodermtasche von Petromyzon nach Kupffer) über- und umwachsen, und so einen medianen Zellkomplex bilden, aus dessen hinterer

(2) Its connecting stalk is axial in position (van Wijhe, '82); dorsal to carotis (Dohrn, '88). (3) This section of the head cavity is so similar to the remaining sections, that it must be considered as serially homologous with them (Balfour, '81). Oppel ('90, p. 623), however, states (for Anguis) that "nur der histologische Bau und die Art der ersten Entstehung dieser vorübergehend im Mesoderm auftretenden Somiten gestattet, an der Deutung festzuhalten dass es sich hier in der That um Somiten handelt."

That the 1st cavity is ventral would seem to follow from the evidence that (1) it arises as an entodermic diverticulum from the prechordal portion of the alimentary canal (Seessel'sche Tasche), whose cavity is at first continuous with that of the alimentary canal (Kastschenko, '88, Kupffer, '88, '90, '93). "Streng genommen," says Froriep ('92^{a}, p. 589), "konnte es übrigens immer noch eher ventral, als dorsal genannt werden, wenigstens was sein Lumen und seine untere Wand anlangt. Denn das Aequivalent der Chorda, welche als Achsenfaden dorsale und ventrale Gebilde scheidet, ist selbstverständlich nur in der oberen Wand des medianen Verbindungsstückes zu suchen."[1] (2) The method of separation of the premandibular head cavity from the entoderm, as well as the presence of a median connecting stalk, serves to distinguish this from the following mesoderm segments (Kupffer, '93). (3) According to Kupffer ('94) the connecting stalk of the premandibular cavity is

---

Hälfte für jede Seite ein Somit entsteht (van Wijhe's erster), während die vordere Hälfte zu Grunde geht." It is readily seen that this evidence tells decidedly against the view that the connecting stalk is ventral, and against the view of Kupffer and Froriep, that its lumen is a part of the archenteron.

Furthermore, Goette ('90) has given evidences concerning the method of formation of the anterior mesoderm in Ammocœtes which stands in direct contradiction with that stated by Kupffer, and, if true, takes away the chief support of the theory of the visceral-pouch nature of the anterior mesoderm in that animal. Goette writes: "Unbedingt muss ich aber die angeblichen 'Coelomdivertikel' des Urdarms im Kopf und Vorderumpf für täuschende Bilder erklären, was sich am Besten versteht, sobald man die Mesodermbildung durch die ganzen Schnittserien von vorn nach hinten verfolgt und dabei die vollkommene Uebereinstimmung derselben in allen Regionen antrifft. Ein Blick auf die Abbildungen lehrt, dass von einer verschiedenen Auffassung derselben nicht die Rede sein kann: giebt es im Rumpf keine Coelomdivertikel, so fehlen sie auch im Kopf. Auch die beiden 'präoralen Kopfhöhlen' sind weiter nichts als das erste Mesomerenpaar, welches allerdings wenn man seine erste Anlage in unmittelbarer Fortsetzung der folgenden Mesomeren übersah, später eine Ausstülpung des Urdarms vortäuschen kann, wie ich es weiter oben auseinandersetzte." Goette's figures, especially Figures 42, 43, and 44, strongly support his statements.

[1] Willey ('94, p. 175) accepts Kupffer's and Froriep's conclusions.

ventral to the dorsal aorta.[1] The vessel which Dohrn ('88) called the *carotis,* and which he stated lay ventral to the connecting stalk of the first cavity, if comparable at all, is comparable only to the *carotis ventralis* of Amniota.[2]

The chief arguments concerning the nature of the 2d (mandibular) cavity have already been given in connection with the general question of the pre-otic mesodermal segments, and it is therefore not necessary to repeat them here. The evidence of a continuous lumen between this cavity and the alimentary canal stated by Miss Platt ('91^a) has been interpreted by her as favoring the view that the cavity is formed as an outgrowth from the dorsal wall of the alimentary canal, similar to the mesodermal pouches in Amphioxus. Kupffer ('94), however, regards it as evidence in favor of his view, that these cavities are abortive visceral pouches. It is necessary, finally, to recapitulate a point in evidence which has only an indirect bearing on the question of the somatic value of the 1st, 2d, and 3d cavities, but which concerns vitally the morphology of the eye muscles (derived in Selachii from these cavities). It has been stated by Hatschek ('92) and Kupffer ('92–'96) for Ammocœtes (Petromyzon Planeri). Their results tend to show that the eye muscles of that low Vertebrate are, with the possible exception of the musc. rectus posterior (externus), derived from splanchnic and not from somatic mesoderm. According to Hatschek ('92), the musc. obliquus superior appears as a differentiated portion of the muscles of the velum, which correspond with the musc. adductores mandibulæ. His evidence (pp. 149, 150) is as follows: "Vom vorderen inneren Rande dieses Muskels [velar muscle] dringt nämlich ein Muskelfaserbündel dorsal in das Bindegewebe ein und zieht seitlich am Trabekel vorbei zwischen dem ersten und zweiten Trigeminusganglion hindurch bis in die Nähe des Auges, wo es im Bindegewebe zugespitzt endet. Von da beginnt — wie ein zweiter Muskelbauch — mit seinem zugespitzten hinteren Ende der musc. obliquus superior und zieht, wieder anschwellend, in gleicher Richtung weiter zum Auge. Die histologische Uebereinstimmung beider

---

[1] Kupffer's statement applies to that cavity in Ammocœtes which has been homologized, in my opinion correctly, by most investigators (Balfour, Dohrn, Shipley '87, Kupffer) with the premandibular cavity of Selachii.

[2] In my opinion those writers who have quoted Balfour ('81) and Marshall ('81) as holding that the connecting stalk of the premandibular (1st) cavity is ventral have misunderstood them. They both spoke of the two lateral parts of this cavity as prolonged ventralwards to meet below the base of the forebrain. They give no proof that the stalk is morphologically ventral, and in my opinion speak of it as ventral only with reference to the wall of the brain.

Muskelteile ist eine vollkommene. Dieses Verhältnis ähnelt in hohem Grade jenem, welches van Wijhe als ein embryonales von den Selachiern abgebildet hat. Seine Deutung ist aber darin zu korrigieren, dass der m. obliqu. sup. nicht dem parachordalen Muskelblatte, sondern den Seitenplatten zugehört. Die übrigen Augenmuskeln, die in Form eines Kegelmantels an der medialen ventralen Seite des Augapfels sich finden, bilden in Bezug auf ihre Lage und histologische Beschaffenheit eine dritte Gruppe, deren Ableitung nicht ganz sicher erscheint. Sie sind wahrscheinlich von den Konstriktoren des Visceral-apparates abzuleiten. Keinesfalls können sie nach ihre Lage, Verlaufsrichtung und Struktur zu den Seitenrumpfmuskeln in Beziehung gebracht werden."

Kupffer's ('94) results are essentially a confirmation of those of Hatschek. Finding that the premandibular cavity entirely disappears, and that its cells contribute in no part to the formation of the eye muscles, Kupffer is led to doubt the conclusions of those investigators who derive the muscles innervated by the oculomotorius from the epithelium of this cavity. According to Kupffer all the eye muscles (with the possible exception of the musc. rectus posterior) are derived from two visceral arches, the "trabecular" and the mandibular. This evidence, as well as that given by Hatschek, obviously stands in direct contradiction to the somite theory. I am, however, after my study of the literature, inclined to be optimistic concerning the ultimate settlement of the question as to the somatic value of the pre-otic mesodermal segments, for the differences of opinion are not due to equivocal evidence, but to directly contradictory and equally positive statements. We have chiefly to determine who has stated the facts correctly in order to determine whether we shall accept the opinion of van Wijhe, or that of Kastschenko, Rabl, and Froriep. The evidence obtained by me, which leads me unhesitatingly to accept the view of the first, that the head somites are serially homologous with trunk somites, is as follows. I find the preotic mesodermal segments as described by van Wijhe ('82) most clearly defined by mesodermal constrictions or clefts in embryos of Squalus with 28 or 30 somites (Plate **3**, Fig. 13, Plate **6**, Fig. 40, Plate **7**, Fig. 46).[1] They are so distinctly marked that they may be seen in whole specimens properly cleared, as well as in sections. Moreover, they are found to be the same on both sides of the embryo.[2]

---

[1] Van Wijhe's post-otic mesoderm segments have indisputable somatic value, and need not be brought into discussion.

[2] An examination of some finely preserved embryos of Torpedo ocellata, kindly given me by my friend, Professor A. N. Sewertzoff, leads me to agree with Sedg-

The contention that the constrictions between van Wijhe's somites are incomplete does not appear to me to militate greatly against the view that they have morphological value, inasmuch as their permanency has been repeatedly attested (van Wijhe, Hoffmann, Neal, and Sewertzoff). Nor does Rabl apparently consider this argument as of great weight, since he regards van Wijhe's 5th (1st post-otic) somite — though the constrictions which are found in front and behind are incomplete — as a true somite. The reduction in the myotomic portion of the dorsal mesoderm accounts in great part for the incompleteness of the constrictions. I believe that one who follows the development of the pre-otic and sub-otic mesoderm in Ammocœtes, and observes the ontogenetic dissolution of the compact dorsal mesoderm into loose mesenchyma, which follows the great enlargement of the nerve ganglia and of the otic capsule, is in a position to understand the reduction of the dorsal mesoderm in this region in Vertebrates higher in the phylogenetic scale than Ammocœtes.[1]

wick ('92), that this is not true of the mesoderm segments discovered by Dohrn ('90, '90ª) in that form. Dohrn apparently did not endeavor to ascertain whether they were symmetrical or not. I am unable to determine, even in carefully made reconstructions of well oriented frontal sections of embryos at the same stage of development as that described and figured by Dohrn ('90ª), whether or not there is a correspondence of the mesodermal segments on the two sides of the head anterior to the one which, in my opinion, corresponds with the 15th segment of Dohrn. While my own negative conclusions cannot be regarded as in any sense disproof of the segmental value of Dohrn's somites, it is my opinion that the evidence of their variability shown by the conflicting results of Killian ('91) tends to throw considerable doubt upon it. Since Killian ('91, p. 103) finds that of the anterior of these segments one is to be regarded as the sclerotome portion of a somite, while others are simply vesicular enlargements of the mesoderm of the mandibular arch, it is to be inferred that Dohrn subjected the head somites of Torpedo to little critical examination. To regard as evidence of somites all vacuolar spaces in the dorsal (and lateral!) mesoderm which appear between the somatopleure and splanchnopleure at the time these layers separate, seems to be too uncritical. Similar phenomena appear in the mesoderm of Squalus in those early stages of development, when the cœlom is in the process of formation, viz. in stages when the neural plate is widely expanded and the embryo possesses 4 or 5 somites. Recent studies by Sewertzoff ('98) render still more doubtful the results of Dohrn and Killian.

[1] A mechanical explanation of the constrictions between the head somites of van Wijhe, such as that offered, but without evidence, by Kastschenko ('88), seems hardly worthy of consideration. That such constrictions as those, for example, between somites 3 and 4, and 4 and 5, cannot result from the so called mechanical influence of visceral clefts, follows from the evidence already stated by Hoffmann ('94 and '96) that in Squalus, the constrictions lie dorsal to the visceral arches. I cannot, however, agree with Hoffmann that we may conclude from this evidence that the visceral arches are intersomitic in position, as are the ribs in the

The evidences of irregularity in size and discontinuity in development and differentiation are not, in my opinion, the more serious of the objections raised. Such differences may indeed be explained as cœnogenetic. Rabl himself has given the evidence ('89) that the first rudimentary visceral cleft is differentiated later than the second. Moreover, it is well known that the first rudimentary myotome in Amphioxus develops later than the following. Differences in time of development and of differentiation are to be expected when a comparison is made between the Anlagen of serial organs, some of which become highly differentiated (e. g. the eye muscle somites, 1st, 2d, and 3d), while the others (e. g. the anterior, the 4th, and the 5th somites) are becoming rudimentary. It is interesting to find that the last intersomitic constrictions to be formed are those between the anterior and the 1st cavity, and between somites 4 and 5, that is, the constrictions separating the most rudimentary somites. The separation of the anterior somite from the premandibular is first complete in an embryo with 26 or 27 somites, while the constriction between somites 4 and 5 appears first in an embryo with 28 somites. Consequently van Wijhe's statement, that the segmentation of the dorsal mesoderm begins in the neck region and proceeds continuously anteriorly and posteriorly, is true only in part. But it also follows that the discontinuity in the development of the more anterior constrictions may be explained as in great measure due to degeneration. The retardation in development due to degeneration, already apparent in the 1st somite of Amphioxus, makes itself manifest in the somites of the more highly specialized Squalus as far posteriorly as the 7th somite of van Wijhe (equivalent to the 8th somite of Amphioxus ?), which I believe to be *the first somite differentiated, as well as the first to develop a permanent myotome.*[1] The correlation between degeneration and retarded development serves to explain, for the occipital somites at least, why the development of the somites in the Craniota begins in the neck

---

trunk. Such purely topographic relations in the Selachian cannot be regarded as weighty evidence in the settlement of this question, in comparison with the evidence stated for Amphioxus (van Wijhe, '93, Hatschek, '92), Bdellostoma (Price, '96^a), and Amphibia (Houssay, '91, Platt, '94), which has led these investigators to regard the visceral clefts as intersomitic in position. In view of the great probability of a shoving forward of the visceral clefts with reference to the somites in Squalus, I am unable to accept Hoffmann's conclusion on the basis of the evidence he presents.

[1] On account of the considerable variation in the length of embryos in early stages of development, I am unable to state positively that the seventh somite is the first to develop. It may be the eighth somite which does so, as stated by Hoffmann ('94, '96). The seventh somite shows some signs of degeneration, having a small myotome and losing its ventral nerve during development.

region. So far as I know, hitherto no explanation of this phenomenon has been suggested.

That which I have regarded as the more serious of the objections made by Rabl ('89 and '92), viz. that the pre-otic segments are not morphologically comparable with trunk somites, inasmuch as they do not show a differentiation into myotome and sclerotome, may be met by a denial of the statement, so far as it applies to the 3d somite of van Wijhe.[1] I have followed the development of this somite through closely connected stages of development, until it becomes converted into the musc. rectus posterior and assumes relation with the eye, in order to determine whether in its development it exhibits those marked differences which, as stated by Rabl, serve to distinguish pre-otic and post-otic mesodermal segments. The evidence which I have obtained may be summarized as follows: Cross sections of embryos in early stages of development leave no doubt that the 3d somite, as its topographical relations to chorda, dorsal aorta, epibranchial line, and dorsal wall of alimentary canal show, is composed of only dorsal mesoderm. Figure A represents a cross section in the region of this somite from an embryo with 28 somites (compare Plate **3**, Fig. 13). It is seen that a well marked cavity (myocœl), surrounded by a single layer of epithelial cells, may be distinguished.[2]

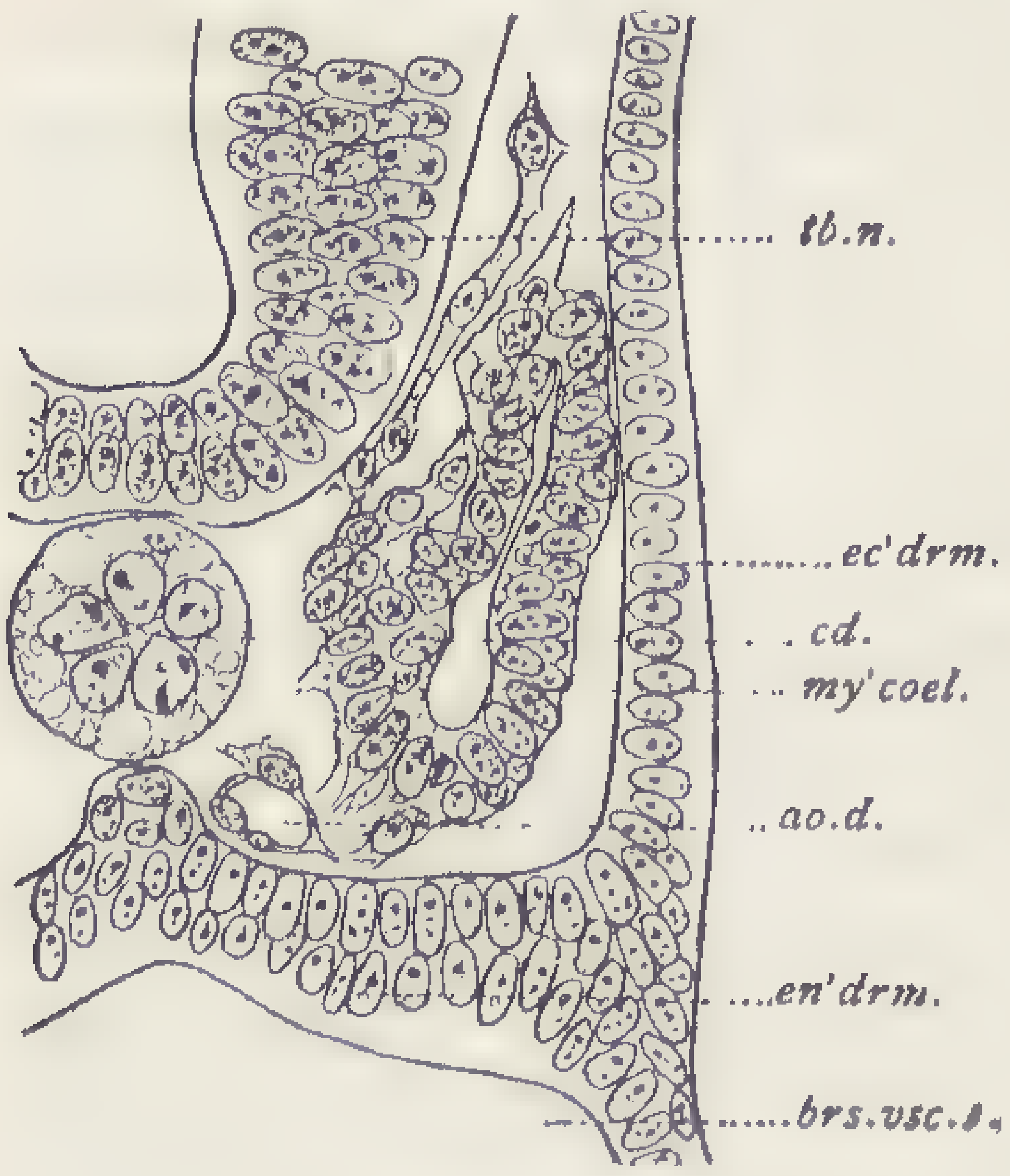


Figure A.

---

[1] Both van Wijhe ('82) and Killian ('91) have affirmed a differentiation of head segments into myotome and sclerotome.

[2] That the epithelial walls of the cavity (Fig. A) are not continuous with the two layers of the lateral plates is due to the obliteration of these two layers caused by the great development of the first visceral pouch.

Fig. A. Cross section of a Squalus embryo in the region of van Wijhe's 3d somite and encephalomere IV. × 240. The dorsal nature of this mesodermal segment is attested by its relations to dorsal aorta and wall of alimentary tract. At this stage (Acranienstadium) the region of proliferation of mesenchyma is seen to be a definite one, and to correspond in its relations with the sclerotome of trunk somites.

ao. d., dorsal aorta; *brs. vsc. 1*, first visceral pouch; *cd.*, chorda dorsalis; *ec'drm.*, ectoderm; *en'drm.*, entoderm; *my'cœl.*, myocœl, enlarged ventrally to form a sclerotome vesicle; *tb. n.*, neural tube.

The cavity of the somite is enlarged ventrally opposite that portion of its median surface where a rapid proliferation and migration of cells appears to take place. I see no reason why the more dorsal and lateral portion of the mesoderm should not be homologized with the myotome portion, and the ventral median region with the sclerotome portion of trunk somites. I am unable to detect any essential difference between the phenomena presented in this section and those presented in sections made in the region of van Wijhe's 5th and 6th somites, to which Rabl grants "Bürgerrecht" as true somites. The greater dorsal extent of the latter cannot be regarded as an essential difference. Here, as there, we find a well marked and definite region of cell proliferation. As development goes on, the cavity of the 3d somite increases in volume, and at the same time the somite grows forward, chiefly by the elongation of its anterior end, median to the Gasserian ganglion. In confirmation of the statement of Miss Platt ('91), I find that the first muscle cells are differentiated in the median wall of that portion of the somite which at this stage lies posterior to the Gasserian ganglion. The great extension of the anterior portion seems to retard its histological differentiation. But in this portion also, when muscle cells appear, they are found in the median wall. Rabl ('89, p. 236) says: "Während ferner die Muskulatur der Urwirbel ausschliesslich aus der medialen Wand entsteht, nimmt sie im Vorderkopf zum grössten Theil aus der lateralen und zum kleineren Theil aus der hinteren Wand der sogenannten Somite den Ursprung." A cross section of the myotome of the 3d somite at a late stage of development appears to me to refute this statement (Figure B). It is clear from an examination of the phenomena presented in such a

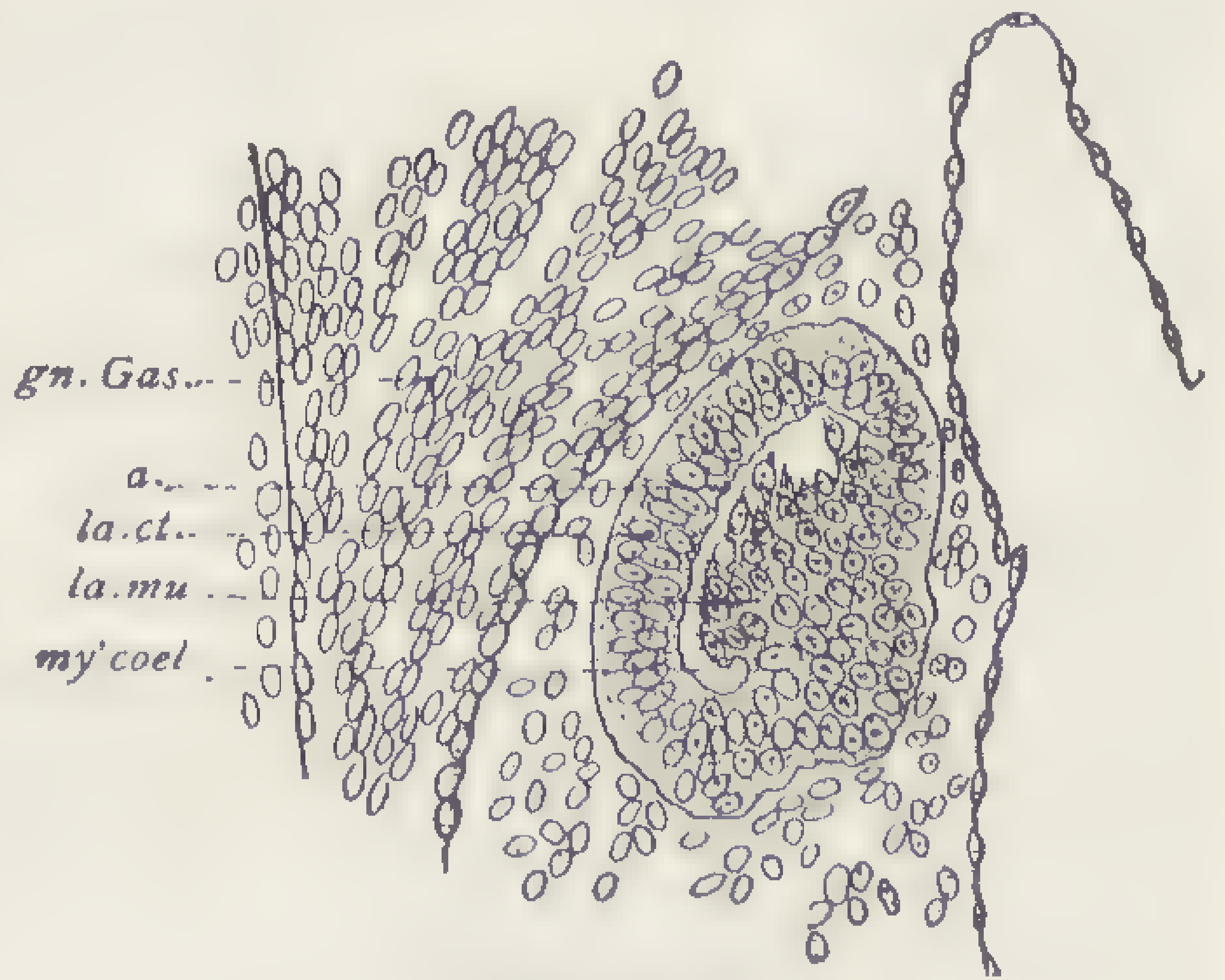


FIGURE B.

FIG. B. Portion of a cross section through the middle of the myotome of van Wijhe's 3d somite, in a late stage of development (20 mm.). Elongated muscle cells are already differentiated in the median wall (muscle plate), while the lateral wall (cutis plate) retains its epithelial character. × 50.

a, cell migrating from the median wall of the myotome into the myocœl; *gn. Gas.*, Gasserian ganglion; *la. ct.*, cutis plate; *la. mu.*, muscle plate; *my'cœl.*, myocœl.

section, that the greater part of the cells proliferated into the cavity of the myotome, the cells of which are at this stage already converted into elongated muscle cells, arise from its median wall. While the outer wall still maintains its primitive epithelial character, the inner wall has become many cells in thickness and some of these cells appear in the act of migrating into the now greatly diminished lumen of the cavity. Later, however, the cells of the outer wall also are converted into muscle cells, and thus both walls of the cavity participate in the formation of the musc. rectus posterior. We have therefore in the 3d somite of van Wijhe a pre-otic segment of the dorsal mesoderm, which becomes differentiated into myotome and sclerotome, and whose musculature is derived in greater part from its median wall. Furthermore, as is well known, its musculature is innervated by a nerve (abducens) which all the later morphologists, with, so far as I know, one exception (Kupffer, '94, '95), regard as a ventral nerve comparable with spinal ventral nerves. Finding this to be the case with at least one pre-otic mesoderm segment, we are in a better position than we otherwise should be to understand the more modified, or at least more divergent, conditions presented by the remaining pre-otic segments, viz. the anterior, the 1st, the 2d, and the 4th. That in these segments marked peculiarities appear is certain. In the 4th somite we have a segment of the dorsal mesoderm divided by constrictions from the 3d and 5th somites at a time when it presents essentially the same evidences of differentiation into myotome and sclerotome which appear in the 3d and 5th somites. That no muscle cells are formed in its inner wall, and that it soon breaks up into loose mesenchyma, are phenomena which are to be expected in a somite destined to become rudimentary. That it is more rudimentary than the 5th somite is due to the development of the otic capsule, under which it lies. The 5th somite — in whose inner wall elongated cells appear, without however developing into muscle fibres (as stated by Sedgwick, '92) — thus forms a natural transition to the conditions presented by the 4th. If the 3d and 5th are to rank as somites, it is in my opinion impossible to deny that the 4th, which lies between them, is serially homologous with them, even though it should lack some of the characteristics of a typical trunk somite.

Passing forward in the embryo to the 2d (mandibular) somite, it seems to me indisputable that this is the anterior continuation of the dorsal mesoderm. In very early stages it grows ventrally to form the mesoderm (mesothelium) of the mandibular arch, a process which, according to Kupffer ('88), occurs in Petromyzon also. However, only the dorsal part of the "mandibular cavity," which later becomes separated from the ventral to form the musc. obliquus superior, can by virtue of its topographic relations to chorda and aorta be regarded as the somatic portion of this mesoderm segment (Plate **7**, Fig. 56). Its ventral portion, which later becomes differentiated into the musc. adductor mandibulæ, is therefore splanchnic. While the indications of the differentiation of the 2d somite into myotome and sclerotome are less clearly expressed than in the case of the 3d and 4th, I have no reason to question the correctness of Killian's ('91) interpretation that such appear. The great enlargement of the cavity of the somite is the chief factor in modifying its form and the relations of its constituent parts. While Miss Platt ('91) finds the musculature to arise first in the median wall of the somite, that is to say, the *dorsal* part of the so called "mandibular cavity," Hoffmann ('96) states that the musc. obliquus superior arises in its upper and lateral walls. In my opinion their conclusions are not so divergent as they might at first sight seem to be, for I believe that the portion of the somite which Hoffmann calls dorsal is morphologically *median;* in other words, that it is the portion which in early stages lies against the wall of the neural tube (Plate **7**, Fig. 56). I agree with Hoffmann that the musc. obliquus superior arises in the dorsal and lateral walls of the second (van Wijhe's) somite, but with the qualification that the dorsal wall is morphologically median.[1]

The first (premandibular) somite shows in its development even greater peculiarities than those of the mandibular; yet it appears to me to possess somatic value as unquestionably as the latter does. The first and most important question to answer is whether this segment represents dorsal mesoderm or a diverticulum from the alimentary canal, and for this purpose the relations of the connecting stalk furnish us with the decisive evidence. In a median sagittal section of an embryo with 14 or 15 somites, such as that shown in Figure C, the tissue which is later differentiated as the connecting stalk of the first somite appears as a mass of cells between the base of the brain, in that region which lies just posterior to the pit of the infundibulum, and the dorsal wall of the alimentary canal. Posteriorly this mass of cells is continued into the chorda and its relations are seen to be such that, if the chorda is dorsal, so must the mass of cells be also. The lumen of the alimentary canal may be traced to a point directly ventral to the pit of the infundibulum, where it ends as the so called "Seessel'sche Tasche" (Kupffer's "präorale Darm"), while its walls become continuous anteriorly with that mass of tissue which later differentiates into the "anterior cavities." Furthermore, a cross section of a corresponding stage of development in a plane immediately posterior to the infundibulum (i. e. along the line $\alpha\ \beta$ of Figure C) gives equally convincing evidence (shown in Figure D) that the mass of cells (1) lies *dorsal* to the wall of the alimentary canal, with which, however, they are in close connection in this somewhat earlier stage (11–12 somites). There exists not the faintest shadow of evidence that the mass of cells which forms in its lateral part the premandibular cavities and in its median part their connecting stalk, represents entodermal diverticula. During development, as the result of the ventral growth of the infundibulum, the pre-oral (Seessel's) pouch becomes obliterated and the mass of cells surrounding the "anterior cavity" is cut off from those posterior to the infundibulum (26–27 somites). By this change in relations the Anlagen of the connecting stalk and of the premandibular cavity take a position apparently *anterior* to the alimentary canal and in close

---

[1] Miss Platt's ('91ᵃ) evidence of the continuity of the cavity of the alimentary canal and that of the mandibular cavity, as well as her evidence of two segments in the latter, appears to me illusory.

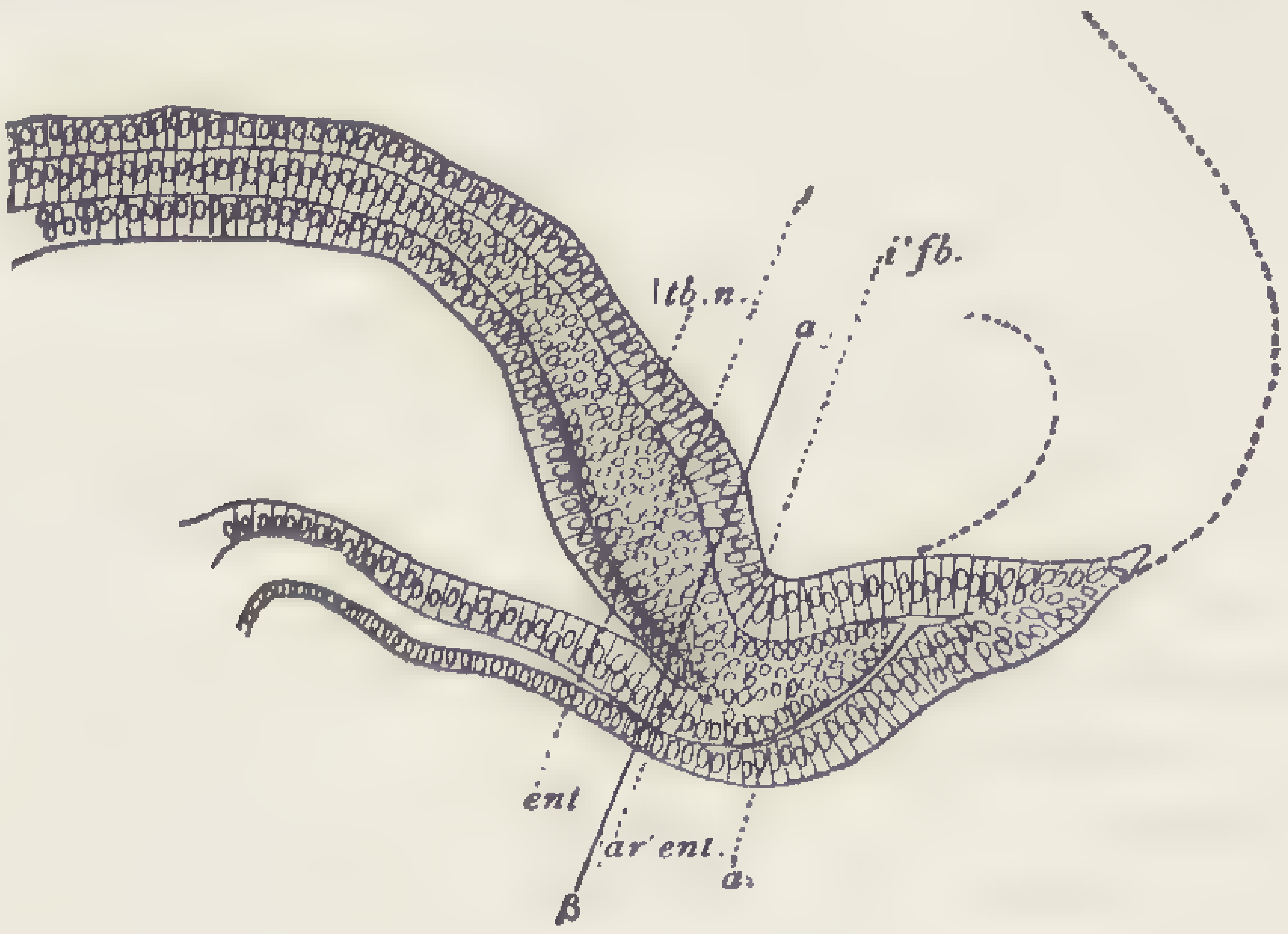


FIGURE C.

FIG. C. Median sagittal section of a Squalus embryo with 14 or 15 somites. The neural folds have not as yet met in the mid-dorsal line. × 77. The mesoderm of the connecting stalk of van Wijhe's first somite is seen as a thickened mass of cells lying between the base of the brain and the dorsal wall of the alimentary tract.

1, mesoderm which later becomes differentiated as the connecting stalk of the first head cavity. *a*, mesoderm of the "anterior cavity" (Platt); *ar'ent.*, pre-oral pouch of the archenteron; *ent.*, dorsal wall of alimentary canal; *i'fb.*, infundibulum; *tb. n.*, ventral wall of the neural tube; $\alpha\ \beta$, projection of plane of the section shown in Figure D.

connection with the ectoderm immediately posterior to the infundibulum. Still later (40 somites) cavities appear both in the median connecting stalk and in the lateral mesoderm, and these by their fusion form the continuous cavity in the manner already described by Miss Platt ('91^a). It follows therefore that the premandibular cavities comprise dorsal and only dorsal mesoderm,[1]

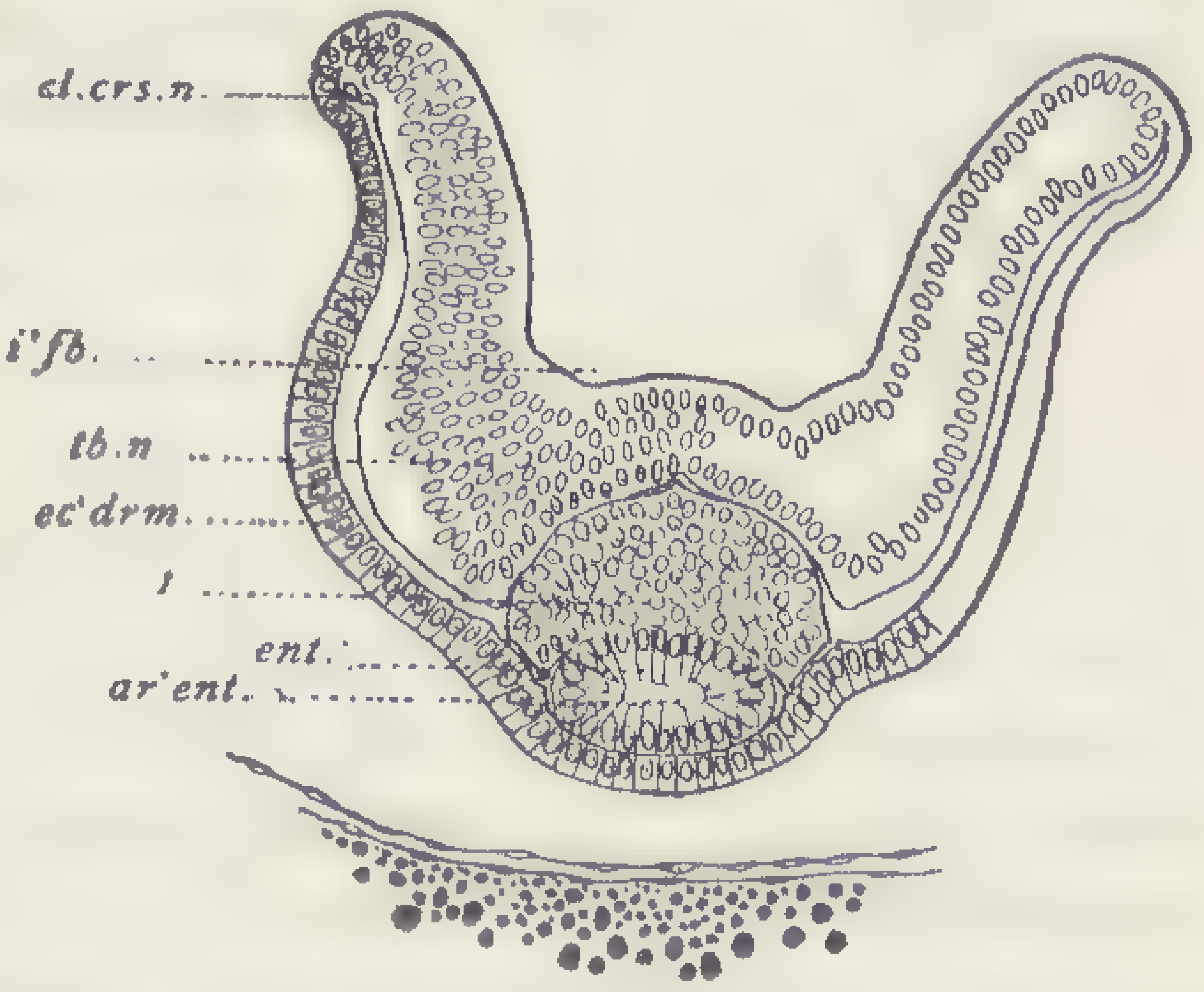


FIGURE D.

---

[1] Hoffmann ('94, p. 648), however, finds evidence of a splanchnic portion of the premandibular somite in a "Zellstrang, welcher dem Mandibularbogen parallel verläuft und der Vorderfläche deises Bogens unmittelbar aufliegt" (his Fig. 4 x, p. 648). He adds, "Ein Lumen dieses Bogens habe ich im diesem Strange nie gesehen," and he uses this evidence to support his conclusion that the mandibular arch is double. I can confirm Hoffmann's statement as to the presence of this "Zellstrang" in the anterior portion of the mandibular arch; but there is another cord, not mentioned by Hoffmann, which is in every respect similar to this one and extends parallel and close to the *posterior* wall of the arch. I hold Hoffmann's interpretation, however, to be incorrect, since, according to my determination, the cells of these strands are in large part if not entirely ectodermal in origin, i. e derivatives of the neural crest. The cells of the Anlage of the Trigeminus may be followed in closely connected stages as they migrate ventrad until they enter the mandibular arch, where they come to surround the mesothelium as a ring of loose cells between the mesothelium and the superficial ectoderm. This evidence confirms the previous results of Kastschenko, Platt, and Goronowitsch ('93). While the fate of these cells is not clear to me, Miss Platt ('94 and '97) finds that in Necturus they contribute in large part to the formation of the cartilage of the mandibular arch. Considering the similarity in the origin of the anterior and posterior cell strands, as seen in parasagittal sections through the mandibular arch, it becomes noteworthy that Hoffmann ('94) in his preliminary paper failed entirely to reproduce in his figures the posterior, while in his later paper ('96, Taf. III. Fig. 22), he figures two cell strands as histologically quite different from each other. This appears to me a notable illustration of the prejudicial influence of a theory. Although I

FIG. D. Cross section of a Squalus embryo with 11 or 12 somites in a plane corresponding with that of the line $\alpha\ \beta$ of Fig. C. × 50. The section shows clearly the dorsal position of the connecting stalk of van Wijhe's first somite (I) in relation to the pre-oral pouch (*ar'ent.*).

I, mesoderm of the connecting stalk of van Wijhe's first somite; *ar'ent.*, archenteron = pre-oral pouch; *cl. crs. n.*, neural-crest cells; *ec'drm.*, ectoderm; *ent.*, entoderm; *i'fb.*, infundibulum; *tb. n.*, neural tube.

and it may also be inferred that the median portion of the connecting stalk is morphologically the undifferentiated anterior portion of the chorda, while the more lateral portions of the connecting stalk may be regarded, as they have been by Killian ('91, p. 102), as representing the sclerotome of the somite. Furthermore, the inference drawn by Froriep ('92^a), on the ground of evidence presented by Kastschenko ('88) and Kupffer ('88, '90, '94), that the lumen of the connecting stalk must be ventral and morphologically a part of the procœlom, receives no support. If Kupffer's statement that the premandibular cavities of Ammocœtes are formed as diverticula from the alimentary canal is correct, their development in Ammocœtes must differ essentially from that in Squalus. Goette ('90), however, flatly contradicts Kupffer's statements. My own observations on Ammocœtes lead me unhesitatingly to accept the evidence presented by Goette.[1] Besides, the criteria furnished by the study of the early stages of development of the premandibular cavity in Squalus seem to me more satisfactory, because more decisive, than the evidence used by Kupffer ('93^a, p. 522) to demonstrate the ventral nature of the connecting stalk of the premandibular cavities in Ammocœtes, viz. the relation to a blood-vessel which is only hypothetically the complete homologue of the dorsal aorta. I find this blood-vessel in embryos of Ammocœtes of somewhat advanced stages of development (4 mm.) extending above the connecting stalk of the premandibular cavities, as the apparent anterior continuation of the dorsal aorta, as stated by Kupffer. But there is also ventral to the connecting stalk a similar blood-vessel, which unites with the dorsal vessel both anterior and posterior to the connecting stalk. It is consequently difficult for me to comprehend why the more dorsal vessel rather than the more ventral one is to be regarded as the anterior continuation of the dorsal aorta. Kupffer gives no reasons, simply stating that the ventral vessel can be homologized, if at all, with the carotis ventralis of Mammalia. Now, if we are to apply rigidly such a criterion as Kupffer's to

---

am unable to accept Hoffmann's conclusion on the basis of the evidence he presents, I believe there are good grounds for holding that a visceral arch, which once existed between the mandibular and the hyoid (first and second visceral) arches, has disappeared in phylogeny. The evidence in favor of this view will be summarized later.

[1] That Kupffer has not in his studies come to a right understanding of the development of the anterior head mesoderm seems to me certain from a comparison of my sections with those figured by him ('90, Figg. 31 und 32, Taf. 28). The cells which he calls ganglionic are in my opinion the anterior mesoderm. This appears to me to be Kupffer's fundamental error.

determine what is dorsal and what is ventral, it would follow from the evidence already stated by Platt ('91) that the anterior portion of the dorsal aorta in Squalus embryos comes to lie in part *dorsal* to the chorda, and therefore that this organ, commonly known as chorda *dorsalis*, could more correctly be named chorda *ventralis*. Kupffer's argument thus leads to a *reductio ad absurdum*.

According to Hoffmann ('96) the muscles innervated by the oculomotorius have their origin from the posterior part ("Fortsatz") of the premandibular cavity. Because of the complicated development and the secondary subdivisions of this cavity, it is difficult to be certain; yet it seems to me that, as in the case of the second and third cavities, the epithelium of both median and lateral walls participates in the production of the muscles formed from this cavity, viz. musc. obliquus inferior, and recti inferior, superior, and anterior.

Before passing to a consideration of the nature of the "anterior cavities," I wish to discuss, in connection with the preceding study of the morphology of the eye-muscle somites in Squalus, the evidence of the development of the eye muscles of Petromyzon which has been given by Hatschek ('92) and Kupffer ('94), and to determine in how far this brings us to an understanding of the morphology of the eye muscles in Vertebrates in general. The repeated confirmation of Marshall's conclusion that the eye muscles in Selachii and Reptilia are derived from the epithelium of the first, second, and third cavities — van Wijhe ('82), Dohrn ('85), Orr ('87), Kastschenko ('88), Miss Platt ('91), Oppel ('92), Hoffmann ('96), and myself — seems sufficient to remove any doubt (so far as those groups of animals are concerned) which Kupffer ('94) may have sought to throw upon that conclusion. In Amphibia, Birds, and Mammals, as is well known, the eye muscles are differentiated from the connective-tissue capsule surrounding the eye. Although the source of these cells is not known with certainty, there is no reason to doubt that, as in Selachii and Reptilia, they have their origin from the dorsal mesoderm. In direct contradiction to these facts, which hold true for higher Vertebrates, stand the conclusions of Hatschek and Kupffer, that in Cyclostomes the eye muscles are splanchnic in their origin, i. e. derived from the mesoderm of the visceral arches. Let us examine the evidence given by them, in order to determine in how far it seems to warrant their conclusions. Hatschek's briefly summarized evidence has been stated on pages 192, 193, and needs no repetition.

In sections of a 5 cm. Ammocœtes I find the relationship of the median posterior musculature of the eye capsule to the velar muscle, which is the probable homologue of the musc. adductor mandibulæ of Selachii, to be those stated by Hatschek. Whether in this muscle group we have to do with the musc. obliquus superior, I am not able to state, since its innervation still remains uncertain to me.[1] I know, however, that it is not innervated by the oculomotorius. Its fibres, moreover, are not continuous with those of the velar muscle at this stage of development, if indeed they are at any stage. Hatschek's chief evidence that this muscle is derived from the velar muscle apparently consists in their histological resemblance, which he states is complete. At the stage studied by me this is certainly untrue. For I find that while the velar muscle is composed of large fibres, at least 7μ in diameter, the fibres of the muscle in question are in their widest part not over 3μ in diameter, and also that, while the fibres of the former show well marked longitudinal and cross striations, those of the latter show these very faintly. Moreover, the nuclei of the former are for the most part round or oval, while those of the latter are exceedingly elongated. It is of course possible that Hatschek bases his statements on the examination of the histological conditions in embryos of a different stage of development. But even if we grant that the musc. obliquus superior in Cyclostomes is, as in the Selachii, derived from the dorsal part of the musculature of the mandibular arch, this evidence no more warrants the conclusion that the muscle is splanchnic in origin in the former group than in the latter. Of its dorsal origin and somatic nature in the latter group, proof has been given above.

Even more theoretical than his conclusions concerning the origin of the musc. obliquus superior appears Hatschek's inference that the eye muscles innervated by the oculomotorius are derived from the constrictors of the visceral arches, a conclusion which he draws apparently by the method of exclusion. It does not seem to have occurred to him that these muscles may have had their origin from the connective-tissue capsule of the eye, the cells of which are in my opinion derived from the dorsal mesoderm in this region, which in early stages becomes disintegrated and surrounds the eye vesicle. Kupffer ('94) thinks that the more difficult part of the task of tracing the development of the eye musculature in Ammocœtes is accomplished when he has followed the growth of muscle cells from the so called "Trabekular" and the mandibular arches until they come into close relation with the eye capsule in a 6 mm. embryo. In consideration of the facts that he does not even know that these muscle cells become differentiated into the eye muscles, and that he has not determined their innervation, the doubt which he seeks to throw upon the results which differ from his own appears quite unwarranted. Furthermore, I find that the anterior and posterior velar muscle strands described by Kupffer are in essentially the same relations to the eye capsule in stages of 6–9 mm. as in those of 5 cm., and that these strands show no relation — except that relation of the posterior (mandibular) muscle strand described by Hatschek ('92) — to the eye muscles, which are already clearly differentiated in the latter stage. I must therefore conclude that Kupffer has not seen the early stages of the development of the eye muscles of Ammocœtes. I regard the determination of their origin in this animal as an embryological task yet to be accomplished, — a task in which the well known difficulty of obtaining material in stages between 9 mm. and 30 mm. will be encountered. For it is in these stages, in my opinion, that the eye muscles are differentiated.

---

[1] That Hatschek ('92) incorrectly identified the musc. rectus posterior, has been shown by M. Fürbringer ('97) from the study of its innervation, a matter to which Hatschek seems to have paid no attention.

I turn now to the development of the "anterior cavity," which has been so thoroughly studied by Miss Platt ('91, '91^a) and by Hoffmann ('96) that I need say but little, and that of a general nature. It seems very clear, since the "anterior" mesoderm segment develops from a perfectly solid mass of cells anterior and lateral to the infundibulum of the brain, that the statement of their formation as lateral diverticula of the alimentary canal is purely hypothetical. It seems also warrantable to infer that the connecting stalk which unites the lateral halves of the segments in early stages of development, the cells of which according to Hoffmann ('96) entirely disappear, represents in part the anterior continuation of the alimentary canal. But it is impossible to state, because of want of such criteria as chorda and dorsal aorta, whether we have here to do with dorsal mesoderm. Without proof to the contrary, and with the evidence that these cavities assume a histological appearance similar to that of the following ones, I conclude with Platt and Hoffmann that the "anterior" mesoderm segment, which appears, so far as is known, in only two Selachii (Squalus and Galeus), is serially homologous with those behind it. I am able to confirm the evidence given by these two observers, that mesenchyma cells migrate into the lumen of the cavity in the later stages of its development, and to confirm the former, that such cells first migrate from the median wall (Figure E), in which also some cells assume an elongated spindle form, possibly indicating rudimentary muscle cells. Such histological evidence would seem to tell in favor of the view that this mesoderm segment, like the following ones, is to be regarded as of somatic value.[1]

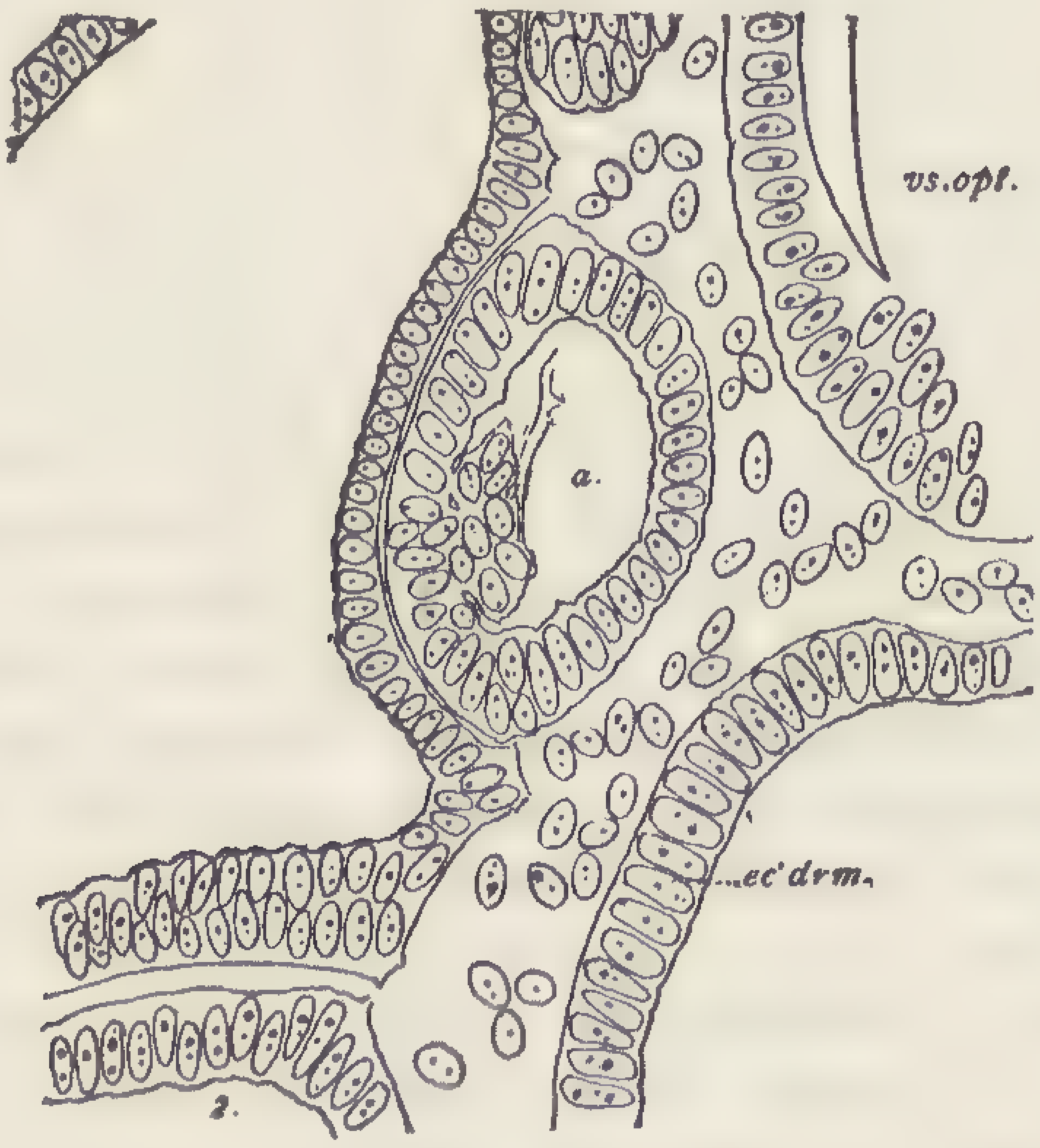


FIGURE E.

d. SUMMARY.

Neuromeres and somites show an exact numerical correspondence throughout the length of the embryo. The serial alternation of myelomeres and somites evinces the metamerism of the former, while the exact numerical correspondence of the encephalomeres and head somites appears equally convincing evidence of the metameric value of the encephalomeres. The head somites in Squalus are homologous with those described by van Wijhe ('82) for Scyllium and Pristiurus, and there is yet another anterior to these, viz. the "anterior" somite first

---

[1] As the most anterior of the cavities of the Selachian embryo, it would seem more probable that the anterior cavities described by Miss Platt should be homologized with the "head cavities" (vordere Entodermtasche) of Amphioxus, than that the next following, the premandibular, should be.

FIG. E. A cross section through the "anterior cavity" (frontal section of the embryo) in an embryo with 78 somites. × 240. To show the proliferation of cells into the myocœl from the median wall of the cavity.

1, 2, first and second head cavities; *a*, "anterior cavity" (Platt); *ec'drm.*, ectoderm; *vs. opt.*, optic vesicle.

seen by van Wijhe in Galeus. The somatic value of the post-otic head somites is indisputable. The pre-otic somites, five in all, are also in my opinion homodynamous with trunk somites. They are segments of the dorsal mesoderm (with the possible exception of the "anterior"), which, as exemplified in the third somite (van Wijhe's), become differentiated into myotome and sclerotome. While the "anterior" and the fourth somites become rudimentary and develop no muscle fibres, the eye muscles are differentiated from the median and lateral walls of the first, second, and third. The eye muscles of Selachii are therefore somatic in their origin, not splanchnic,[1] as has been held by Hatschek ('92) and Kupffer ('94). It will furthermore be shown that the nerves which supply them are serially homologous with ventral spinal nerves. It is to the consideration of the nerve relations that I now pass.

VI. The Relation of Neuromeres to Nerves.

Ahlborn ('84^a) said: "Es bleibt auch im Auge zu behalten, dass die gesammte Neuromerie secundärer Natur ist: sie ist nur eine Wiederhohlung aller vor ihr entstandenen Metamerien des Körpers. Eine primäre Metamerie, wie sie z. B. im dorsalen Mesoderm vorliegt, ist weder im centralen, noch im periferischen Nerven-system vorhanden,[2] und wenn im Rumpfe die Neuromerie mit der primären Mesomerie übereinstimmt, so reicht diese Eigenschaft im Allgemeinen nur so weit, als die Nerven sich innerhalb des primär segmentirten Mesoderms befinden, und sie hört auf, wenn die Nerven in solche Organe eintreten, die ausserhalb der Mesomeren liegen, oder die in einer anderen nicht segmentalen Metamerie entwickelt sind."

In the trunk, the arrangement both of myelomeres and nerves is clearly metameric, being correlated with the segmentation of the mesoderm. Related to each mesodermal somite is a ventral nerve (motor root), which arises from segmentally arranged groups of ganglionic cells in the anterior (ventral) horn of the spinal cord, that is, from each myelomere. Into the posterior (dorsal) horn pass the fibres of the dorsal nerve, which have their peripheral distribution in the skin of that segment (rami cutanei) and in the intestine (sensor and motor sympathetic fibres).

In a study of the simple, and it has been assumed primitive relations in the trunk, it is important to consider not only the peripheral distribution of nerve fibres, but also their distribution in the central nervous system. Gaskell ('89) has rightly insisted that the position of the cell groups which are in connection with the nerve fibres, is the true criterion of what forms a nervous metamere, rather than the position of the exits of the nerve fibres. The shifting of nerve roots is too well known to need discussion here. In regard to sensor nerves Miss Platt ('96) says: "Both development and comparative anatomy tend to show that it is a matter of little moment whether these fibres [of the lateral-line nerves] enter the brain by one nerve root or another." I find as a result of my own studies that the ganglionic cells of cranial nerves enter into fibrillar relation with the neural tube at points quite widely separated from the encephalomere from which the cells were proliferated, and also that in embryos of different Vertebrates the relations of the fibres of the same nerves to the encephalomeres are variable, not only in the case of ganglionic roots but of medullary roots also, as those of the trigeminus, abducens, and glossopharyngeus. In the swine and the chick the abducens arises from encephalomere VI, whereas in S. acanthias it is in relation with encephalomere VII. Also in swine and chick the root of the glossopharyngeus is in relation with encephalomere VII, whereas in S. acanthias it passes from the neural tube posterior to this neuromere. It is obvious, then, that we must take into consideration, particularly in the case of cranial nerves, both the location of the "Kerne" of the medullary roots, and the points or regions of proliferation of the ganglionic cells of ganglionic roots, in order to determine their primitive relationships.

---

[1] With the exception of the musc. rectus posterior (Hatschek).

[2] Compare Froriep ('94).

a. Historical Review.

An examination of the literature bearing on the question of the relation of nerves to neuromeres is rendered difficult by the fact that many investigators have failed to distinguish between medullary and ganglionic nerve relations, and thus have not made clear what they meant by the statement that a nerve "develops" from, or has its "origin" from, the expansion or constriction of a neuromere. The figures of McClure ('90) and of Waters ('92), for example, show a proliferation of the ganglionic Anlagen of nerves from the neuromeres, but not the relationship of the neuromeres to *nerve fibres.* While it seems very probable that the proliferation of ganglionic Anlagen has a bearing on the primitive relationship of the dorsal nerves (sensor portion), our best criteria of the segmental value of encephalomeres, as well as of myelomeres, is their relation to medullary nerves, — i. e. ventral nerves and the motor components of the dorsal nerves. Furthermore, we must determine the primitive relations of medullary nerves, not by the place of exit of their fibres (i. e. by their roots), for we know these to be variable, but by the position of their "Kerne" in the walls of the neural tube.[1]

There is considerable difference of opinion as to whether nerves ("roots") arise primarily from the expanded portion of the encephalomere (or myelomere), or from the constrictions between these segments. As early as 1878 Marshall said, "My investigations tend very strongly to prove that all the nerves arise primitively from the widest parts of the dilated vesicles, whether of brain or cord, and never from the intervening constrictions." Later, McClure ('89), who is in agreement with Marshall as well as with Orr, Béraneck, and Waters, said, "The dorsal roots of spinal nerves take their origin from the apex of their respective myelomeres in exactly the same manner as the nerves of the medulla do from their respective encephalomeres." Minot ('92) criticises McClure for overlooking the fact that the "neuromeres can have no genetic relation to the ganglionic nerves." The ground of Minot's statement does not seem to me to be so self-evident as not to be in need of explanation.[2]

In disagreement with McClure, Miss Platt ('89) claimed that "the concavity in both medulla and spinal cord is the source from which the nerve originates," and her conclusion, which Minot accepts, is that the origin from the expanded portion of the neuromere is secondary. In view of this difference of opinion it is of interest that Balfour ('85) stated that in Selachian embryos the dorsal and ventral roots of spinal nerves alternate with each other, the dorsal roots being intersegmental (intersomitic) and the ventral roots segmental (somitic) in position. Miss Platt did not, however, in her statement of nerve relations make a distinction between dorsal and ventral nerves.

---

[1] The most serious obstacle to the use of this criterion is the difficulty of applying it in those early stages of development when metameric relationships appear least modified. Martin ('90 and '91, p. 230) has noted an ontogenetic ventral shifting of motor "Kerne" in the cat.

[2] It is to be regretted that McClure gave no figures of the nerve relations of myelomeres. Minot apparently assumes that the neuromeres are constituted solely in adaptation to a motor segmentation, and therefore that the neuromeres are segmental localizations of ganglionic cells (i. e. motor "Kerne") in the wall of the neural tube, just as are the segmental ganglia of Annelida. It seems to me therefore that McClure might have met Minot's criticism by reminding him that neurologists have recognized in the medulla groupings of ganglion cells which are in relation with sensory fibres, i. e. sensory "Kerne" or "Endkerne" (see Edinger, '96, p. 366), and may well contribute to the metameric enlargements.

b. NERVE RELATIONS IN THE TRUNK OF S. ACANTHIAS.

An examination of sections in the trunk region of embryos of S. acanthias leaves no doubt whatever that the chief proliferation of ganglionic cells occurs in the regions of constriction between myelomeres, i. e. opposite the somites, and that the ventral roots also arise opposite the somites. Motor roots appear long before the sensor roots, as was first stated by Sagemehl ('82). Dohrn has affirmed that they arise as early as Balfour's stage H. I find them in embryos of S. acanthias in which 34 somites are differentiated, stage H. From the very first, i. e. at this early stage, they are in relation with the ventral portion of the neural tube at a point directly opposite the middle of the somite. That the relation with the tube is opposite the *middle of the somite* is most easily demonstrated in frontal sections (see Plate 6, Fig. 42, which represents a frontal section of an embryo with 50 somites); but that their relation is with the *ventral* wall of the tube, is most clearly seen in cross sections (Plate 6, Fig. 41, *rx. v.*). In frontal sections more dorsally situated than those which show the ventral roots, the spinal ganglia are likewise seen to lie opposite the middle of the somites[1] (Plate 6, Fig. 43). In later stages, however, the spinal ganglia lie opposite the anterior portion of the somites, i. e. intersomitic in position, as a result, probably, of the shifting of the somites. Since by this time the constrictions between myelomeres have disappeared, *it is quite impossible to state that dorsal roots arise either from the constrictions or from the dilatations of the myelomeres.*

McClure ('90, p. 42) has said that in the forms studied by him "the dorsal branches of the spinal nerves pass from the external surface of the myelomeres to the space between two somites, which is opposite their point of origin, and fuse with the epiblastic thickenings to form the spinal ganglia." Such a statement, if true, is certainly of great importance in settling the question of the morphology of cranial nerves. For it is now generally stated by morphologists that the chief distinction between spinal and cranial nerves consists in the fact that the ganglia of cranial nerves receive cellular material during development from the ectoderm of the lateral surface of the head, whereas the spinal ganglia do not. So far as I know, McClure's statement remains unconfirmed, and it is certainly not true for Squalus, and not true, so far as I am able to determine, for Amblystoma. In Petromyzon, however, as has been previously stated by Scott ('87) and Shipley ('87), the spinal ganglia lie opposite the constrictions between the somites (in later stages opposite the myosepta).[1] Thus, inasmuch as the dorsal nerves of Ammocœtes are *intersomitic* and never unite with the ventral nerves which are *somitic* in position, and inasmuch as the dorsal ganglia show close connection with the ectoderm in early stages of development and lose this connection during development, the spinal nerves of this animal form a natural transition from the nerves of Amphioxus to those of Squalus and higher Vertebrates. For in Amphioxus ventral nerves are somitic in position, dorsal nerves intersomitic, and the connection of the ganglia of the latter with the skin is retained throughout life.[2] Two chief causes seem to have brought about the change in the relations of the dorsal spinal nerves in the Vertebrate series. The first cause appears to have been the great dorsal and anterior extension of the trunk myotomes, and the second cause the posterior extension of the ramus cutaneus dorsalis vagi (ramus lateralis vagi), which takes the place of the rami cutanei of the spinal nerves. The physiological reason for the extension of the vagus is to be found in the advantage obtained from the centralization of sensory impulses in the brain. With van Wijhe ('92), Hatschek ('93), and M. Fürbringer ('97), I accept the theory of Prochaska, Sömmering, and Gegenbaur that cranial and spinal nerves are homodynamic, and the view of Hatschek ('92) that dorsal and ventral nerves primitively alternated with each other.[3] Of these, the former were mixed in function and the latter motor, as in Amphioxus.

---

[1] Similar relations of dorsal ganglia and ventral roots have been shown by Marshall ('78, Plate III. Figs. 27 and 28) for birds; by Hoffmann ('90, Taf. CLV. Fig. 7) for reptiles; by Dohrn ('91, Taf. V. Figg. 16 und 17) for Selachii; and by Sewertzoff ('95, Taf. V. Fig. 16) for Amphibia.

c. Nerve Relations in the Cephalic Region of S. acanthias.

In the head, where the nerve relations are much more complicated, it will be necessary to trace the development of the nerves in different stages. The series represented in Figures 7 to 21 (Plates **3** and **4**) is intended to show the changes which the neural crest (colored in blue) undergoes, and likewise to show the development of the brain vesicles up to the time when a fibrillar connection of the nerves with the neural tube is effected and the chief peripheral branches are differentiated.[1]

---

[1] Because of this relation to the myomeric constrictions in Ammocœtes and the relation of the ganglia to the *expansions* of the spinal cord (myelomeres) deducible from it, it is obvious that not very great morphological value can be given to the fact that in Squalus the ganglia lie opposite the *constrictions* of the spinal cords.

[2] I hold with Hatschek ('92) and M. Fürbringer ('97) that in Amphioxus the homologues of the dorsal ganglia of Craniota are found in the cell groups at the place where the dorsal nerves meet the skin.

[3] See also Ransom and Thompson ('86).

Minot ('92) and Mitrophanow ('93) have stated that the neural crest in Selachii is not differentiated before the closure of the neural tube, and Rabl ('89) found that in Pristiurus embryos the "Trigeminus Anlage" first appears at a stage with 18 somites. On the other hand, Beard ('88) and Dohrn ('90) have shown that in some Selachii,[2] as well as in Sauropsida, the neural crest is differentiated in the region of the head before the closure of the neural tube.

As has been previously stated, my observations confirm those of Beard and Dohrn, since I find that at an early stage, when the cephalic plate is still widely open, the fundament of the trigeminus is clearly differentiated from that portion of the neural plate which is destined to form the neural tube. The disassociation of the neural-crest cells in this region and their resultant loss of compact arrangement have taken place to a considerable extent before the neural folds meet in the mid-dorsal line. Usually the neural folds first close in the trunk region behind the cephalic plate, and later in the region of the midbrain, i. e. in the region of the "Trigeminus Anlage." The closure of the cephalic plate occurs last in the forebrain, where the "neuropore" persists for a considerable period.

At a stage with 15 or 16 somites (Plate **3**, Fig. 7), when the cephalic plate is closed except in the region of the forebrain, the neural crest is clearly differentiated in that region of the brain which extends from the constriction between forebrain and midbrain to the anterior constriction of hindbrain neuromere (encephalomere) IV, i. e. in the region of the so called cephalic flexure. In the region of encephalomere IV a few cells with protoplasmic processes occur in the space between the neural tube and the overlying ectoderm. These may indicate that at one time this encephalomere was a region of cell proliferation and thus possessed a neural crest; but since the cells soon disappear, and since no new ones take their place, this encephalomere may be said to be a region of the neural tube which now (in S. acanthias) possesses no neural crest. That portion of the neural crest which arises anterior to this neuromere has been variously called "Trigeminus Anlage," "germe du

---

[1] A study of the histogenesis of nerve has been made only in the case of the eye-muscle nerves, whose morphology still remains a matter of much dispute.

[2] I am surprised by Hoffmann's ('94) statement that in S. acanthias the trigeminus Anlage first appears in an embryo with 17 somites, that is, after the closure of the neural tube.

Trijumeau" (Mitrophanow, '93), and "erste periaxiale Strang" (Goronowitsch, '93). Its cells at this stage (15 or 16 somites) have already migrated half way down the side of the neural tube (Fig. 7). In the region of encephalomere V the disassociation of the cells of the neural crest has begun, and the dorsal part of the encephalomere in consequence appears enlarged. A ventral migration of its cells, however, does not take place until a later stage.

In an embryo of 18 or 19 somites (Plate **3**, Fig. 8) two regions of cell proliferation, separated sharply by encephalomere IV, are seen. Mitrophanow ('93) has stated that at the beginning the facialis is not wholly separated from either the trigeminus or the vagus group. I find on the contrary, as already stated, that no neural crest is found in the region of encephalomere IV, and that consequently the "Trigeminus Anlage" is separated by the space of this encephalomere from the posterior portion of the neural crest. Apparently as a consequence of cell proliferation and migration, the dorsal wall of encephalomere III is very thin at this stage, while that of encephalomere IV is considerably thicker and its cells are more compactly arranged. The cells of the neural ridge which form the "Trigeminus Anlage" now extend ventrally as far as van Wijhe's second somite. The second region of cell migration is at this stage sharply confined to encephalomere V. Behind this a disassociation of neural-crest cells has begun in the region of encephalomere VI, but no migration has taken place. From an examination of later stages, the cells proliferated from the region of encephalomere V are easily proved to pass ventrally into the hyoid arch, and to form the ganglionic Anlage of the acustico-facialis. From a study of mitotic cells and from the grouping of cells one is led to believe that the greatest cell proliferation takes place in the posterior part of this neuromere.

It is to be noticed that the advancing ventral end of the ganglionic Anlage extends toward the cleft between van Wijhe's third and fourth somite. Also that cell processes from each of these somites now extend toward the ganglionic Anlage.

When the embryo possesses 19 or 20 somites (Plate **3**, Fig. 9) the "Trigeminus Anlage" shows a differentiation into an anterior smaller portion, which passes in front of the midbrain vesicle toward the optic evagination, and a posterior larger portion, which extends ventrally into the mandibular arch, just beneath the superficial ectoderm and external to the second somite. I am inclined to believe that this division of the Anlage is partly due to the enlargement of the vesicle of the midbrain, since frontal sections show that the lateral wall of the midbrain lies very close to the ectoderm. It is evident that the neural-crest cells migrate around the most expanded portion of the vesicle, so that they come to lie in the regions of constriction anterior and posterior to the dilated vesicle. They migrate, as it were, into the spaces where there is room for them. The cells of these two portions are in continuity dorsally, as in the previous stage. As a result of the expansion of the dorsal wall of the neural tube in the region of encephalomere III, the cells of the neural crest are laterally displaced in this region, so that they appear in optical sagittal section (Fig. 9) to have taken a more ventral position. Mitrophanow ('93) has given the name "le groupe nerveux anterieur" to the anterior smaller portion of the trigeminus Anlage, and states that "dans la plupart des cas, ce groupe est peu séparé" (i. e. from the "groupe du nerf trijumeau"). Coggi ('95) finds that in Torpedo this anterior portion of the trigeminus Anlage arises as a paired structure, the lateral halves of which secondarily unite in the mid-dorsal line; Coggi, however, agrees with Mitrophanow that this anterior part of the trigeminus is at first distinct from the posterior larger portion. In S. acanthias, however, I find that both anterior and posterior parts form at first a continuous neural ridge, which lies dorsal to the midbrain vesicle. Only in later stages does the anterior portion become separated as the so called thalamic nerve. At the stage with 19 or 20 somites the cells proliferated from encephalomere V extend somewhat farther ventrad toward the hyoid arch than in the preceding stage, and at the same time a proliferation of cells from the mesoderm extends dorsad to meet them. The mesodermal cells migrate from both sides of the constriction between van Wijhe's second and third somites, and from them extends a cellular process toward the ganglionic Anlage.[1]

The conditions remain practically unchanged in a stage with 21 or 22 somites (Plate **3**, Fig. 10). The anterior and posterior portions of the trigeminus Anlage now extend into the region ventral to the midbrain vesicle, and are about to unite with each other. The cells in the region of encephalomere III have undergone a still greater lateral displacement, from which one may infer that cells are no longer proliferated from the neural crest of this encephalomere. It is seen that the cells of the acustico-facialis are now united with the cellular process from the mesoderm.[1] This process may be traced dorsally to a point outside of the ganglionic Anlage, i. e. between it and the superficial ectoderm. The future course of the nerve is along the line of the process. Between this and the next succeeding stage, which is represented in Figure 11, the trigeminus Anlage undergoes a considerable change. The anterior (thalamic) and posterior (trigeminal) portions having fused ventrally below the lateral midbrain swelling, now extend ventrad as a continuous sheet with two ventral processes, one reaching into the mandibular arch and the other to a point below the eye vesicle. The anterior (thalamic) portion has assumed a more compact appearance, and extends from the region of the constriction between forebrain and midbrain, both ventrad, to a point above and behind the eye vesicle, — where, as already stated, it meets the anterior prolongation of the trigeminus portion, — and anteriad to a point in front (dorsad) of the eye vesicle. The acusticofacialis Anlage now extends into the hyoid arch, *its position being clearly inter-somitic.* Posteriorly, in the region of encephalomere VI, and to a considerable extent behind this, the cells of the neural crest have begun their ventral migration. At this time, then, a continuous neural ridge or crest extends from the anterior boundary of encephalomere V backward into the region of the spinal cord. In cleared specimens and in parasagittal sections the neural crest cells seem discontinuous in the region of constrictions between encephalomeres IV, V, and VI. Both Rabl ('92) and Hoffmann ('94) have held that the pre-auditory portion of the neural crest is discontinuous with the post-auditory portion, and Rabl considers this another proof that the pre-auditory region is one "sui generis." On the other hand, Dohrn ('90) and Mitrophanow ('93) have stated, like the present author, that they find the crest continuous in the two regions.

---

[1] I have been unable to determine that these mesodermic cells participate in the formation of the Anlage of the nerve. It appears to me, however, that such a response on the part of the somites to the development of a nerve Anlage is a fact which cannot be ignored in dealing with the question of nerve development. See also similar evidence in the description of the development of the trochlearis and oculomotorius.

A well marked proliferation of cells seems to take place in the region of encephalomere VI. These cells may be traced continuously into later stages, until they enter the first branchial arch and form the Anlage of the glossopharyngeus. Since previous investigators, with the exception of Herrick and Broman (see Table II., p. 152), have stated that the glossopharyngeus is related to hindbrain neuromere VII,[2] it seems well to call attention to the fact that the cells of the ganglionic Anlage of this nerve

---

[1] Is this mesodermal process the median branch of Kupffer's typical segmental *nerve?* Its relation to the mesoderm leads me to believe that this is the case. It soon disappears, as stated by Kupffer ('91).

[2] Miss Platt ('89) stated that the glossopharyngeus is connected with the posterior constriction of encephalomere VI.

are proliferated from the region of encephalomere VI, the greatest proliferation occurring, however, as in the case of encephalomere V, in the posterior part of the encephalomere. No previous observer has stated that the cells of the ganglionic Anlage of the ninth nerve are proliferated from encephalomere VI. However, that previous observers have seen the proliferation of cells from this encephalomere is possibly shown by the fact that both Shipley ('87) and Kupffer ('94) have found in Petromyzon, between the Anlagen of the 7th and 9th nerves, a "weak primitive acusticus, which soon vanishes." Hoffmann ('94) stated that in Acanthias embryos with 32 to 35 somites, a new outgrowth appears between the facialis and the glossopharyngeus, which to all appearance is a rudimentary and early aborting segmental nerve. Although Hoffmann published no figures, I infer from his description that this outgrowth, or rudimentary nerve, is that portion of the neural ridge which is proliferated from the region of encephalomere VI. I am at least able to say positively that no other outgrowth of cells takes place just posterior to the Anlage of the acustico-facialis. In the phenomena presented by this outgrowth Hoffmann finds the chief support for his contention that the Anlagen of cranial nerves arise as paired segmental outpocketings of the neural tube, corresponding to, or comparable with, the outgrowth of the eye vesicles. He figures diagrammatically the outgrowth of the neural crest in the region of the glossopharyngeus Anlage as an outpocketing of the dorsal wall of the neural tube possessing a lumen continuous with that of the tube. At no time do I find evidence of a lumen between the neural-crest cells, although in later stages the nuclei in the VII and IX ganglionic Anlagen tend to take a peripheral position.

At a stage with 26 or 27 somites (Plate **3**, Fig. 12) the thalamic portion of the trigeminus Anlage is no longer continuous dorsally with the posterior portion of the Anlage, the cells of which come to lie in the region of constriction between midbrain and hindbrain. The thalamic portion extends from the constriction between primary forebrain and midbrain toward the eye vesicle, just behind which it unites with a line of cells, ectodermal in origin, which extends along the dorsal border of the eye close to the superficial ectoderm. Some of the cells of the trigeminus Anlage now extend into the mandibular arch, and have there come to surround the mandibular mesoderm.

A displacement of the cells of the Anlage of the acustico-facialis and of the glossopharyngeus has begun at this stage. This is clearly to be accounted for by the invagination of the auditory epithelium, which is now beginning opposite encephalomere VI. In parasagittal sections the Anlage of the glossopharyngeus appears clearly distinct from that of the vagus, while in the median plane they are seen to be continuous portions of the neural crest.

When the embryo has 28 to 30 somites (Fig. 13) the conditions, so far as the trigeminus is concerned, are practically unchanged. Neural-crest cells still persist in the regions of constriction between the primary brain vesicles. Thus, three strands of neural-crest cells are seen to lie in the region of constriction between the brain vesicles, just as they do in the trunk between the myelomeres. The ganglionic Anlage of the acustico-facialis, which had fused with the thickened auditory epithelium in the early stages of its development, now, as the nerve Anlage recedes from the ectoderm, retains this connection, forming thus the Anlage of the acusticus. The acusticus therefore in its development and relations resembles a *ramus dorsalis* of a cranial nerve.

The cells of the glossopharyngeus have been further displaced. In all the specimens of this stage which I have examined, two distal portions of the nerve Anlage may be distinguished. The fate of the posterior of these is unknown to me. The cells of the anterior portion pass ventrally into the third visceral arch, and are related to the constriction between van Wijhe's somites 4 and 5. In precisely the same way the Anlage of the seventh nerve occupies the cleft between the third and fourth somites. The advancing ganglionic Anlagen pass close to the superficial ectoderm in the plane of the constrictions between the somites. Similarly the Urvagus Anlage meets the mesoderm at the posterior cleft of the fifth somite. This fact seems to me to be of some importance in considering the question whether the branchial nerves are somitic or intersomitic in position, and to warrant the conclusion that the cranial nerves resemble the dorsal nerves of Amphioxus in being intersomitic, as well as in other respects. At a stage with 33 or 34 somites (Plate **3**, Fig. 14) the trigeminus Anlage retains connection with the mid-dorsal line of the neural tube in only two restricted regions, anteriorly by the "thalamic" portion, and posteriorly (in the region of the constriction between midbrain and hindbrain) by a strand of cells to which Miss Platt has given the name "primary trochlearis." Posteriorly the cells of the trigeminus Anlage are grouped into a somewhat thickened mass opposite the posterior part of encephalomere III, the first indication of the differentiation of the Gasserian ganglion. The Anlagen of the acustico-facialis and the glossopharyngeus have become farther separated by the invagination of the auditory epithelium, the displacement affecting the cells of the glossopharyngeus so much that they now lie opposite encephalomere VII. The two nerve Anlagen, however, usually remain connected with each other dorsally by a thin cellular strand. This strand is wanting in some cases, or may be present on one side of the embryo only. Dohrn ('90) has also stated that the separation of the seventh and ninth nerves is due to the crowding caused by the ear capsule, and he held that the connecting strand of cells was evidence of the original continuity of the neural crest on the dorsal side of the ear. Behind the glossopharyngeus the neural crest extends in unbroken continuity into the trunk, but only its anterior portion, which forms the ganglionic Anlage of the Urvagus, extends ventrally between the mesoderm of the side plates and the superficial ectoderm into the region of the pharynx.

In embryos with 38 or 39 somites (Plate **3**, Fig. 15) the thalamic portion still extends as a compact cellular cord from the region of constriction between forebrain and midbrain to a point above the eye, where it unites with the line of ectodermal cells which in later stages forms the ophthalmicus profundus trigemini. This nerve, because of its relations with the trigeminus, "primary trochlearis," and "thalamic" nerves, is regarded by Marshall ('82) and Miss Platt ('91) as a commissural nerve connecting the three nerves mentioned. It has also been regarded as an independent nerve (van Wijhe, '82, M. Fürbringer, '97), and as a ramus dorsalis either of the trigeminus or the oculomotorius. The acusticofacialis Anlage, opposite encephalomere V, is still in continuity with that of the glossopharyngeus by means of a cellular cord dorsal to the auditory invagination, while the cells of the glossopharyngeus and vagus Anlagen no longer appear to be continuous dorsally, as they were in the previous stage.

At a stage of development when the embryo possesses 42 to 44 somites (Plate **3**, Fig. 16), and when two visceral clefts are formed, both the thalamic and trochlear portions of the trigeminus Anlage are much reduced. In an embryo with 48 somites the thalamic portion consists of a strand or cord of cells which extends dorsally from the ophthalmicus profundus, at a point just above the eyestalk, toward the region of constriction between primary forebrain and midbrain, where the two cellular strands coming from opposite sides of the head unite above the wall of the brain. Because of this union, Coggi ('95) has considered this portion of the trigeminus Anlage as a connective "nerve," uniting the *lateral halves* of the ophthalmicus profundus. Its position in Torpedo, according to Coggi, is anterior to the thalamencephalon. If Coggi is correct, its position in Torpedo is clearly different from that in S. acanthias. Coggi's account differs, however, from that of Dohrn ('90^a), who found its relations in Torpedo to be similar to those described by Miss Platt ('91) for S. acanthias. The relations of the acustico-facialis and glossopharyngeus remain unchanged. For a long time cellular strands persist, showing the primitive relation of these nerves to the constrictions between the encephalomeres IV, V, and VI, respectively.

Some important changes in the relations of the neural-crest cells appear in the next (48-somite) stage, and are shown in Plate **3**, Figure 17. For the first time, we find "fibrillar" connections of the trigeminus Anlage with the neural tube. Protoplasmic or fibrillar processes extend from the cells which lie opposite the constriction between encephalomeres III and IV toward both encephalomeres. It has been stated by some investigators (Miss Platt, '91, Locy, '95), that this nerve has its origin from the constriction between the neuromeres. Two main roots are differentiated later, an anterior, in relation with encephalomere III (the "portio minor"), and a posterior, in relation with encephalomere IV (the "portio major"). The nearness of the ganglion cells to the brain wall renders it impossible for me to determine in which direction, whether toward the brain or toward the ganglion, the fibres are first developed. The two chief roots of the trigeminus have been described for other Vertebrates.

The thalamic and trochlearis portions of the trigeminus Anlage are now much reduced in size, each retaining connection with the rest of the nerve fundament by means of an attenuated protoplasmic fibre. The acustico-facialis Anlage has assumed fibrillar connection with encephalomere V, with which it remains connected until the encephalomere disappears. Marshall and Spencer ('81, p. 481, '86, p. 100) have stated that in Scyllium "there is an important difference between the fifth and seventh nerves, inasmuch as in the former the primary root is lost and the secondary alone retained, whilst in the latter both primary and secondary roots are retained up to stage N, and indeed . . . throughout life. The difference between the roots of the fifth and seventh nerves just noticed does not occur in the chick." They also state that in early stages in Scyllium embryos the fifth nerve arises from the brain by three distinct roots, but that in later stages only two roots are found. Their distinction between primary and secondary nerve "roots" is obviously unnecessary, since the only true "roots" are the so called secondary ones. Before these are established we have to do with neural-crest cells, some of which have been shown to be non-nervous in function, and to contribute to the mesenchyma of the head.[1] The ear capsule now lies with only its anterior portion opposite encephalomere VI. Behind the ear capsule and opposite the posterior portion of encephalomere VII lie the cells of the glossopharyngeus, as yet without fibrillar connections with the neural tube. Behind the glossopharyngeus and now separated from it lie the cells of the vagus, extending ventrally as a broad sheet between the mesoderm and ectoderm into the region of the pharynx, where the Anlage becomes segmented by the formation of the visceral clefts. The trochlear and thalamic portions of the trigeminus soon disappear without assuming fibrillar relation with the neural tube.

At a stage with 52 somites, when the embryo is about 8 mm. in length, the thalamic portion remains as a group of cells lying in the constriction between the forebrain and midbrain vesicles (Plate **4**, Fig. 18), but without connection with the ophthalmicus profundus. It very soon disappears entirely, and I think probably contributes to the loose mesenchyma of this region. In precisely the same way the disassociation of cells of the trochlear portion takes place, scattered clumps of cells indicating its previous extent. The Gasserian ganglion and the ganglion of the ramus ophthalmicus profundus (mesocephalic ganglion) are both clearly differentiated. Three branches of the fifth nerve may now be distinguished, viz. the two sensor branches, r. ophth. profundus and r. maxillaris (inframaxillaris[2] Dohrn), and the mixed mandibular branch. Nerve relations to the neural tube remain the same as in the previous stage.

d. Development of the

1. Oculomotorius.

By the time the embryo has reached the length of 8 mm. (52 somites), the oculomotorius has however appeared as a fibrillar process from the base of the midbrain (encephalomere II, Figures F to H), arising as processes from neuroblast cells in the ventral horn of this encephalomere. Since this nerve throws light on the morphology of the premandibular somite, whose musculature it innervates, its development is of great interest and has been studied by many investigators; viz. Marshall ('81), Rabl ('89), Dohrn ('91), Platt ('91), Mitrophanow ('93), and Sedgwick ('94). Neither Marshall ('81) nor Rabl ('89) saw the early stages of its development, and their conclusions are therefore purely theoretical. Both agree in considering the nerve a derivative of neural-crest cells. Rabl ('89, p. 221) thinks he has some right to bring this portion of the neural crest into genetic connection with these nerves, since the course of the third and fourth nerves in later stages corresponds with a portion of the trigeminus Anlage, which I infer from his description to be the "trochlear" portion. He adds, "Ferner darf ich aus einer Reihe von Beobachtungen, die ich nicht bloss an Selachiern, sondern auch an Vögeln und Säugethieren angestellt habe, schliessen, dass die Oculomotoriuswurzel, die nach dem gesagten Anfangs ebenso wie die des Trochlearis aus der dorsalen Kante des Mittelhirns austreten musste, aus dieser Lage allmählich durch die Ausbildung der Pedunculusbahnen verdrängt und an die ventrale Seite verschoben wird."

---

[1] Kastschenko ('88), Goronowitsch ('92), Miss Platt ('93).

[2] This is, I believe, the nerve which in Ceratodus van Wijhe ('82) named ramus maxillaris superior, which in Amphibia Strong ('95) called accessory branch of the fifth, and Miss Platt ('96) r. buccalis profundus V.

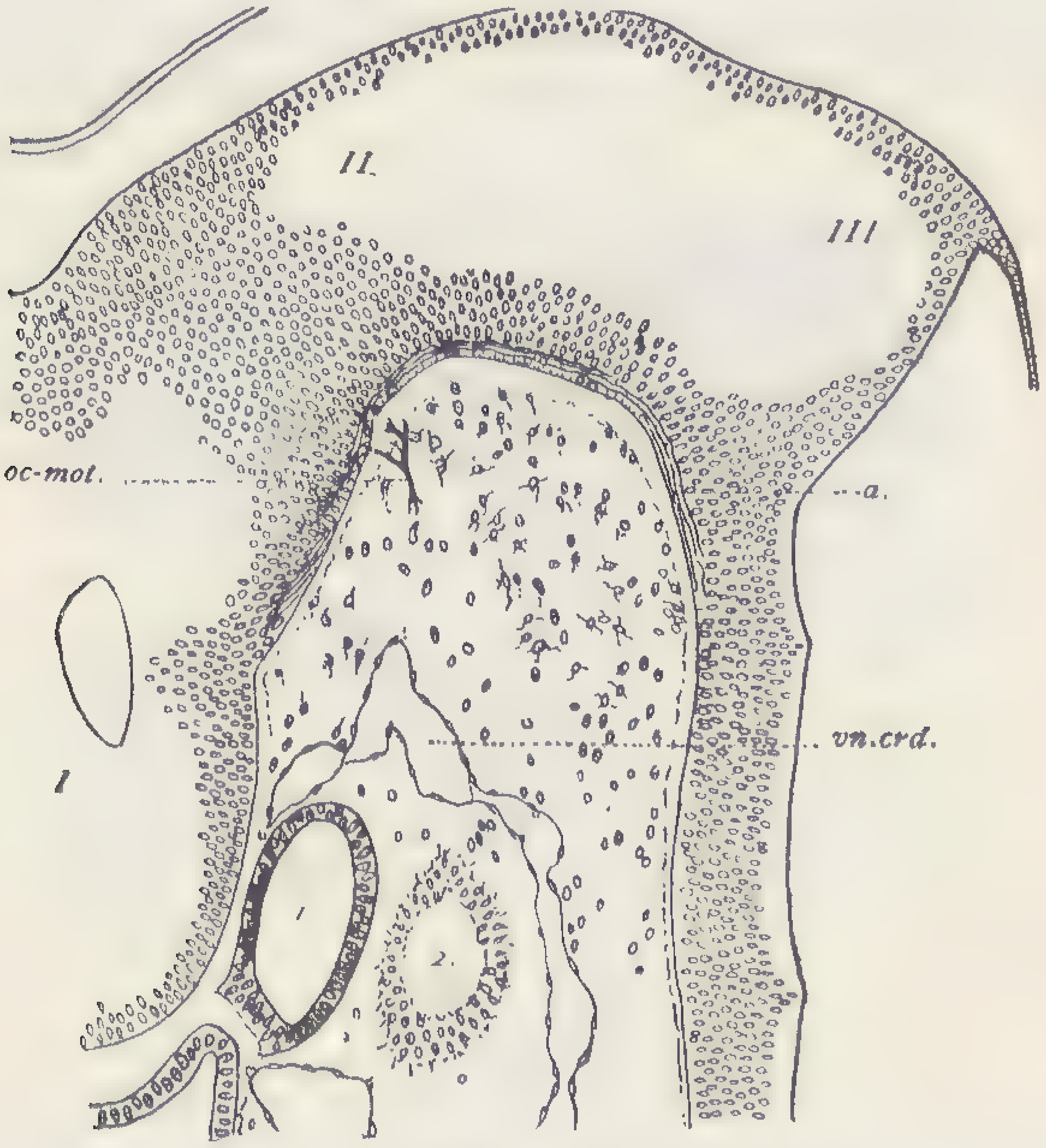


FIGURE F.

FIG. F. Left face of a parasagittal section through the left half of an embryo with 52 somites, showing the relations of the oculomotorius to encephalomere II at this stage. × 50. *I*, *II*, *III*, first, second, and third encephalomeres; 1, 2, van Wijhe's first and second head cavities; *a*, ventral fibre tract; *oc-mot.*, oculomotorius; *vn. crd.*, anterior cardinal vein.

More theoretical and farther from the truth Rabl could scarcely be, yet several investigators have in essential respects confirmed his theory, that the oculomotorius is a derivative of the neural crest. Dohrn's ('91) observations, however, differ fundamentally from those of his predecessors. He sees the beginnings of the oculomotorius in embryos intermediate between Balfour's stages I and K. At first cells in the base of the brain assume a more transparent appearance, and later migrate into the "Randschleier," where they send out processes which unite in a network just outside the base of the brain to form the stem of the nerve. Immediately at the beginning of the outflow of the plasma cells are seen half in and half out of the wall of the tube, and later, but before the oculomotorius has any connection with the mesocephalic ganglion, large deeply staining nuclei are seen in the protoplasmic network which forms the root of the nerve. Dohrn does not lay great stress on the fact that these nuclei are larger than those of the surrounding mesenchyma cells, but from the fact that similar nuclei lie nearer the medullary wall, from which they appear to emerge in increasing numbers during the course of development, he holds the opinion to be permissible, that the nuclei of the early network are emerged medullary elements, and not mesoderm cells which press close to the medullary

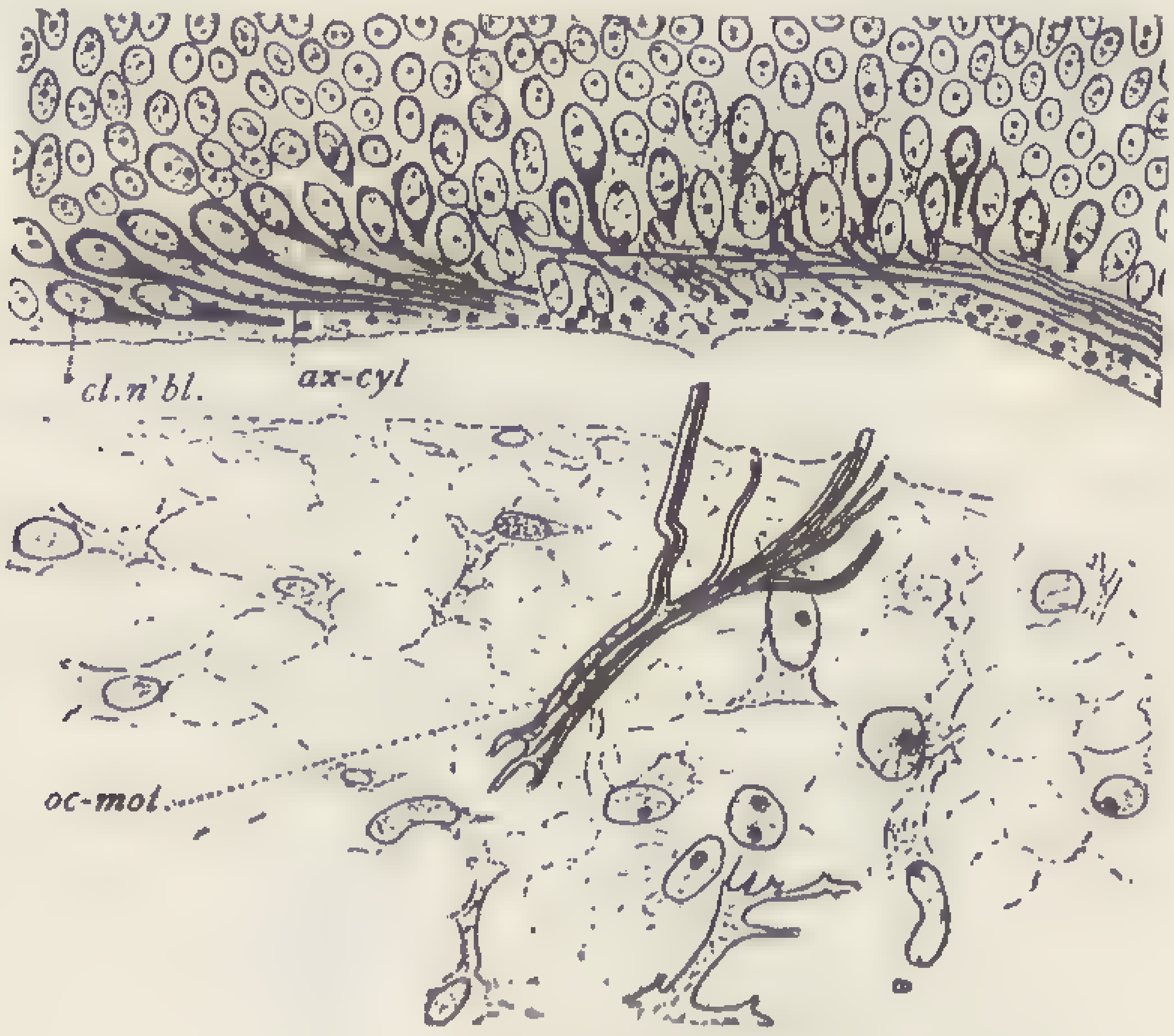


FIGURE G.

FIG. G. A portion of the same section as that shown in Figure F. × 240. The fibrillar nature of the oculomotorius is clearly shown. *ax-cyl.*, axis cylinder process; *cl. n'bl.*, neuroblast cell; *oc-mot.*, oculomotorius.

wall. Dohrn considers it as the *punctum saliens* of the evidence given by him, that ganglion cells and ganglia which may be traced to the adult are to be found in the course of the oculomotorius before this comes into connection with the mesocephalic ganglion, and concludes that such ganglion cells can have had no other source than the ventral horn of the midbrain. He thus takes the view of Balfour, Marshall, Kupffer, and others, that this ventral nerve is formed as a chain of medullary cells, in opposition to the views of His ('89), Kölliker ('92), von Lenhossék ('92), and others, that ventral nerves are formed from *processes* of "neuroblast" cells in the ventral horn of the medullary tube.

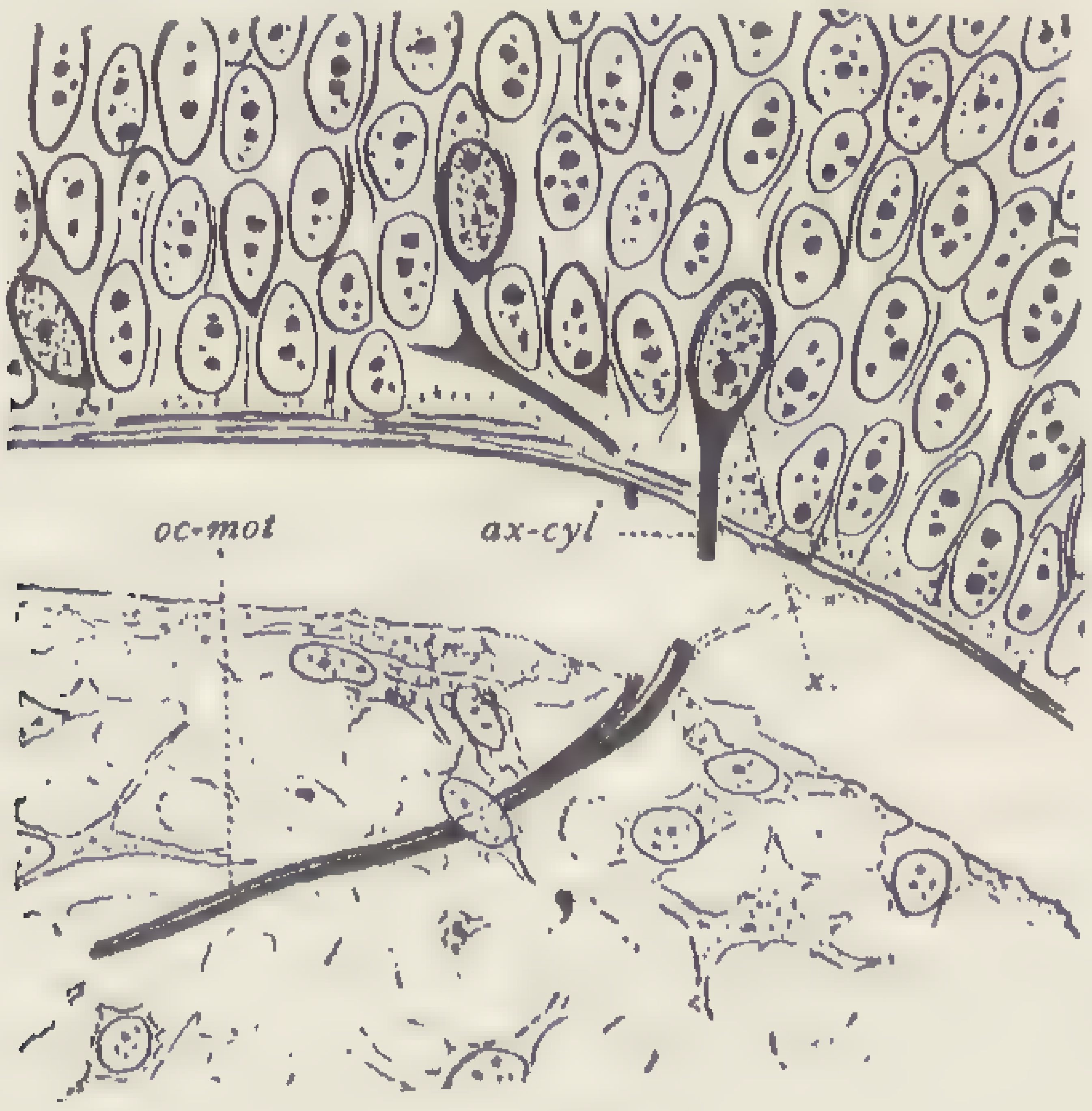


FIGURE H.

Miss Platt ('91) comes to fundamentally different conclusions from those of Dohrn ('91). She finds that the oculomotorius appears first as a single cell proliferated from the mesocephalic (ciliary) ganglion toward the base of the midbrain, with which it at first has no connection. Observations on Squalus, Raja, Pristiurus, and Torpedo convince her that the oculomotorius develops after the type of a sensor nerve [?] by a proliferation of ganglion cells toward the brain wall. Mitrophanow's ('93)

FIG. H. Left face of a parasagittal section through the right half of the same embryo as that represented in Figures F and G, showing the oculomotorius in an early stage of development (52 somites). × 447. The relation of the nerve fibre with an axis-cylinder process from the neuroblast cell x seems clear. *ax-cyl.*, axis-cylinder process; *oc-mot.*, oculomotorius; x, neuroblast cell.

observations confirm those of Miss Platt. According to Sedgwick ('94) the third nerve is formed directly from the neural crest as are the dorsal cranial nerves [?], but arises as a differentiation of the reticulum formed by the breaking up of the neural crest, and first makes its appearance as a projection of nuclei from the mesoceplalic ganglion. His observations thus do not essentially differ from those of Miss Platt, their conclusions differing chiefly by reason of difference in theoretical views as to the mode of nerve development. My own evidence differs quite fundamentally from that given by previous investigators, since I find that the nerve develops after the manner described for spinal ventral nerves in Selachii and other Vertebrates, as an axis-cylinder process from "neuroblast" cells in the ventral horn of the midbrain. At the earliest stage in which I have been able to detect the oculomotorius the extent of its development and its relationships are such as are shown in Figures F to H, which represent sagittal sections of a Squalus embryo with 52 somites (approximately 8 mm. long). At this stage the thalamencephalon is just becoming differentiated from the primary forebrain (encephalomere I). The identification of the fibrillar process as the oculomotorius is made easy by a comparison of its point of attachment, of the direction of its long axis, and of its histological appearance with those of an embryo with 54 somites, where the oculomotorius is already connected with the mesocephalic ganglion. Under higher powers of the microscope the nerve appears as a deeply staining, highly refractive process, clearly distinguishable by these characteristics from the granular and faintly staining processes of the mesenchyma cells at the base of the midbrain. Owing to a shrinkage, which however appears in very few of the specimens killed by the fixing agent used (vom Rath's fluid) and always most markedly in the region ventral to the midbrain, the mesenchyma cells and the roots of attachment of the nerve have broken away from the base of the brain. Since, however, similar deeply staining processes are seen to extend from cells in the ventral horn of the medullary tube towards the points where the roots may be supposed to have once united with the wall of the brain, the inference seems warranted that the nerve is made up of the processes of these cells. The latter show the characteristics described by His ('89) for the neuroblasts of the spinal cord, viz. a highly chromatic nucleus surrounded by a thin, very deeply staining protoplasmic ring, which is prolonged into the axis-cylinder process. The precipitation of osmium serves to render the processes quite opaque and easily traceable among the remaining, as yet undifferentiated, cells of the medullary wall, and to make it possible to determine that other processes, instead of leaving the medullary wall, extend posteriorly in the wall and parallel with it to form the ventral fibre tract. The nerve process (Figure G) shows a differentiation in its distal portion into two deeply staining fibrils surrounded by more faintly staining plasma, the two fibrils dividing distally into three, which enter the fine processes with which the nerve ends. The nerve process on the other side of the same embryo (Figure H) does not, however, show this same evidence of histological differentiation. Here the nerve appears as a highly refractive fibril, and, while having a greater extent than that of its mate of the opposite side, is composed, except at its root, of a single undivided fibril. The connection of this fibril with the axis-cylinder process from a neuroblast cell in the ventral horn seems indisputable, since this passes directly through the limiting membrane at the base of the brain wall, and projects into the shrinkage space directly opposite the chief root of the nerve, as is shown at *ax-cyl.* I have no evidence to offer, such as that stated by His ('88, '89), for Mammals and other Vertebrates, of a migration of the neuroblasts from the "inner layer" of medullary cells, nor do I find any evidence of migration of cells from the neural tube, as stated by Dohrn ('91). I find at this stage neither nuclei connected with the roots of the nerve outside the neural tube, nor such as are half in and half out of the tube.

The connection of the oculomotorius with cells of the mesocephalic ganglion is attained very quickly, and in embryos of 54 or 55 somites has already taken place. At this stage of development, as seen in embryos fixed with the corrosive sublimate-acetic mixture (Davidoff's fluid), the nerve appears (Plate **8**, Fig. 58) as a *cellular* strand, which extends from the inner side of the mesocephalic ganglion toward the ventral wall of the midbrain, with which the nerve unites by at least two main roots. To detect the proximal roots as well as the relations of these with medullary cells, sagittal sections are much more favorable than frontal, since the nerve roots are situated one behind the other.[1] The fact that the nerve is several cells in thickness near the ganglion, while its calibre diminishes as it passes toward the brain wall, would naturally, if one were unacquainted with the conditions shown in the embryo of 52 somites, lead to the inference that the growth of this nerve takes place from the ganglion toward the brain (*vide* Miss Platt, '91, Mitrophanow,

---

[1] Also, for the reason already stated by His ('88^{b}, p. 344) for spinal ventral nerves, that "die Wurzelbündel treten in grösseren Abständen aus dem Rückenmark hervor. Jedes Bündel bezieht seine Fasern aus einem entsprechend breiten Bezirk des Rückenmarks. Die Sammlung derselben erfolgt zum Theil noch innerhalb des Markes, zum Theil erst in der Leibeswand."

'93, Sedgwick, '94). It is interesting to compare the phenomena thus observed in specimens prepared by the Davidoff method with those prepared by the vom Rath method, since the latter clearly differentiates the nerve fibrils, and gives the clue as to the meaning of the cells proliferated from the mesocephalic ganglion. Figure I is drawn from a sagittal section of an embryo with 55 somites killed by the vom Rath method, and fortunately so oriented as to show the oculomotorius in its course from the inner side of the mesocephalic ganglion to a point very near the brain wall. The nerve itself is composed of three deeply impregnated fibrils, which near the brain wall are closely united to one another, while peripherally they become separated. Two lightly staining cells with granular protoplasm lie closely adherent to the nerve, and with low powers are indistinguishable from it. Others appear in the process of migration from the mesocephalic ganglion to assume similar relation. Whether these cells become elements of the oculomotorius ganglion, which would thus conform in its mode of development to the type of a sympathetic ganglion,[1] or whether they form the nuclei of Schwann's sheath, I am not at present in a position to state, since I have not been able to trace their fate. It is of course possible that they contribute to both ganglion and sheath. Whether cells from the mesenchyma in this region contribute to both of these ends, seems to me a question of not great morphological importance, since in my opinion these cells are in great measure, if not entirely, derivatives from the neural crest, and thus *ectodermal*, not mesodermal, in origin. From the evidence thus stated it is seen that the oculomotorius must be

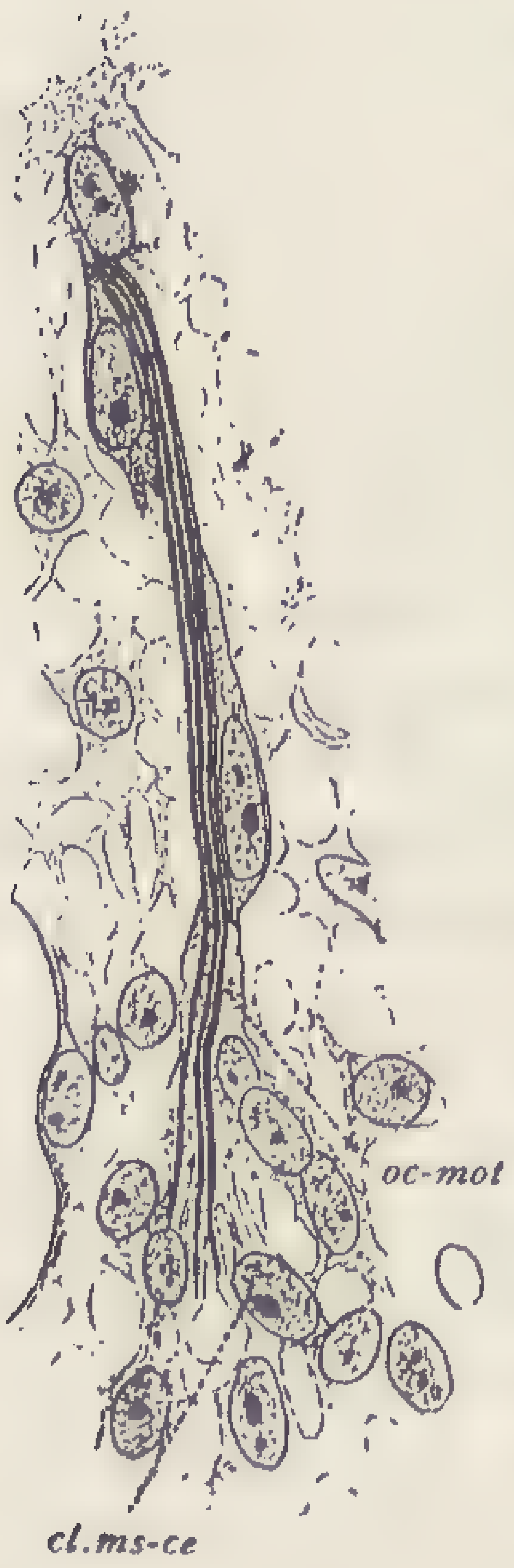


FIGURE I.

---

[1] Many investigators (Rüdinger, Arnold, Gegenbaur, Schwalbe, Hoffmann, Onodi, van Wijhe, Dohrn, Beard, Ewart) have, on histological and embryological grounds, agreed that this ganglion belongs to the sympathetic system.

FIG. I. Sagittal section of a Squalus embryo with 55 somites, showing the oculomotorius in its course from the mesocephalic ganglion toward the brain. × 477. The fibrillar nerve and the peripheral nuclei may easily be distinguished. *cl. ms-ce.*, migratory cell from the mesocephalic ganglion; *oc-mot.*, fibres of the oculomotorius.

regarded as from the earliest stages of development a fibrillar nerve formed by axis-cylinder processes of medullary cells, and that it is no more to be regarded as a *cellular* process or *cellular* nerve in its earlier than in its later stages. The unfavorableness for purposes of nerve study of material killed, with the fixing agents commonly used, has been the chief cause which has kept us so long from the true understanding of the method of the development of the oculomotorius in Selachii. I was at first disposed to consider as of some morphological importance the fact that in stages of development before the appearance of the oculomotorius a process extends from the mesocephalic ganglion to the premandibular somite (Plate **8**, Fig. 61). Its earlier appearance precluding the view that this process has connection with the oculomotorius, I concluded that it furnishes us with evidence of a primitive relation of the ramus opthalmicus profundus with this somite (Plate **8**, Fig. 61). The observations of J. Müller in 1840, P. Fürbringer ('75), Price ('96), and Max Fürbringer ('97), have established that this nerve possesses motor fibres in the Myxinoids, confirming van Wijhe's view of its segmental value. I am, however, not inclined to lay stress on the fact mentioned above as confirmatory of this view, since in later stages (65 somites) I also find a similar process, apparently in connection with the "anterior cavity" (Plate **4**, Fig. 19).[1]

At a stage with 65 somites (10 mm.) the relations of the trigeminus are unchanged (compare Plate **4**, Fig. 19). The r. ophthalmicus profundus trigemini is well differentiated, and shows a marked fibrillar structure, especially clear in embryos killed with vom Rath's fluid. The nuclei seen along the trunk of the nerve are distinctly peripheral in relation to the nerve fibres. The facialis nerve (VII) now possesses four branches, viz. the sensor acusticus branch, connected with the median and ventral side of the otic capsule; the mixed hyoid nerve, innervating the muscles and skin of the 2d visceral (hyoid) arch; the r. ophthalmicus superficialis VII (ophthalmic branch of the 2d trigeminal root of older anatomists), whose sensor fibres develop in close connection with the skin along what in the head corresponds with the dorso-lateral line of the trunk; and the r. buccalis VII (incorrectly called supramaxillaris V by Wiedersheim), developing along the medio-lateral line of the head.

---

[1] Allis ('97, p. 742) also describes in Amia calva a small and apparently degenerating nerve in connection with the ganglion of the profundus. He however, on grounds of the topographical relation of the eye-muscle nerves (III and IV), regards this nerve as homologous with the ophthalmicus profundus trigemini.

The glossopharyngeus is now in fibrillar connection with the lateral walls of the neural tube at a point behind encephalomere VII. The fibres from the ganglion cells of the vagus enter the neural tube at a point somewhat behind the point of origin of the glossopharyngeus. The cells of the two nerve Anlagen, however, still appear continuous. Posteriorly, and at the same level as the origin of the roots of nerves IX and X, the neural-crest cells appear as a commissure (*coms. d.*) connecting the vagus Anlage with the ganglia of the dorsal spinal nerves Ventrally the vagus divides into four mixed (post trematic) branches, each of which innervates the skin and musculature of a visceral arch, and posteriorly is continued beneath the skin as the ramus lateralis vagi along the medio-lateral line.[1]

At this stage, I find the first evidence of the olfactory nerve (I) in the form of connecting strands or fibres between the anterior lateral wall of the forebrain (prosencephalon) and the thickened lateral epithelium of the olfactory plate. The connection between the median portion of the "Riechplatte" and the brain wall (neuropore) has disappeared at a somewhat earlier period (8–9 mm.). According to Marshall ('78) and Beard ('85) the olfactory nerve develops, as do the other dorsal cranial nerves, from cells of the neural crest, and is therefore regarded by them as a nerve morphologically comparable with the dorsal cranial nerves. The evidence given by van Wijhe ('86^a) and Hoffmann ('96), however, serves in the opinion of these investigators to render this view improbable. Van Wijhe ('86^a, p. 680) states that "das Riechorgan und der Nerv entstehen beide aus dem vorderen Neuroporus. Der Olfactorius entwickelt sich nicht aus der Nervenleiste, denn er tritt in einer Periode auf, wann dieselbe im Kopfe schon längst geschwunden ist; auch ist er von Anfang an mit der Haut in Verbindung und unterscheidet sich durch diese zwei Merkmale von allen übrigen dorsalen Nervenwurzeln. Der Riechnerv entsteht also erst nach dem Acranienstadium und in Uebereinstimmung damit ist seine Abwesenheit beim Amphioxus."

Confirmatory of this view is the evidence given by Hoffmann ('96, p. 272) that "der Riechnerv fehlt [in Squalus] aber bis zu diesem Entwicklungsstadium [10–12 mm.] noch vollständig und erst bei Embryonen, welche eine Länge von 13½–14 mm. erreicht haben, beginnt er sich anzulegen. Bis zu dieser Periode liegt die Riechgrube der Medullarwand immer noch unmittelbar an, dies ist auch jetzt noch grösstentheils der Fall, aber mit ihrem medialen Rand fängt sie jetzt an sich von der Gehirnwand zurückzuziehen, bleibt aber mit ihr durch einen kurzen, dicken Zellstrang kontinuirlich verbunden. Dieser Zellstrang bildet die Anlage des Nervus olfactorius, aber es ist nicht möglich zu sagen, welchen Antheil die Epidermis und welchen das Gehirn an der Anlage der Riechnerven nimmt, denn er entsteht aus dem letzten Rest des kontinuirlichen Zusammenhanges von Epidermis und Medullarwand, welcher von Anfang an bestanden hat."

---

[1] Squalus possesses no *dorso*-lateral line nerve corresponding with that of Cyclostomata, Dipnoi, and Ganoidei. I also find no evidence in Squalus such as that found by Miss Platt ('94) in Necturus, to show that there once existed a *ventro*-lateral line in Vertebrates.

His ('89ª) had previously found in the human embryo that the first step in the formation of the olfactory nerve was the migration of mesenchymatous cells between the olfactory plate and wall of the brain. Later the olfactory ganglion is formed by the migration of cells from the lateral walls of the olfactory epithelium. Finally, the olfactory nerve results from the assumption by these cells of a bipolar form and the elongation of the poles both centripetally and centrifugally to form fibrillar connection with brain and olfactory pits.

My own observations concerning the development of the olfactorius are as yet incomplete, and I am not able to add much to the evidence which has been given. In agreement with Hoffmann ('96) I find that, as the olfactory plate and the brain wall separate, they retain connection with each other by faintly staining fibrils in the region of the future olfactory pits. Whether these fibrils enter into the formation of the definitive olfactorius I am not able to state, and the observations of Hoffmann appear to me insufficient to establish this fact. My results and those of Hoffmann do not agree; for he finds in embryos of 16 mm., and still more clearly in embryos of 18–20 mm., that *mesenchymatous* tissue "schiebt sich von allen Seiten zwischen Medullarwand und basale Nasengrubewand ein, und in demselben Grade als beide sich entfernen, nimmt natürlich der Riechnerv an Länge zu." I infer this mesenchymatous tissue to be the same as that which Hoffmann previously states to be derived from the "anterior head cavities." My observations, however, lead me to agree with Marshall ('78), that the cells which appear between the nasal pit and the brain wall, as these separate, are neural-crest cells. Van Wijhe may be technically correct in stating that the neural crest has disappeared in the region of the forebrain at the time when the olfactory nerve is established; but it is certainly not true that the neural-crest *cells* in the region of the forebrain have done so at this stage. They persist in the region of the forebrain which lies opposite and anterior to the optic vesicle, and in my opinion are the cells which migrate between olfactory pit and brain wall as these separate from each other. I regret that I am not yet in position to describe the later differentiation of these cells, but it appears to me not improbable that they enter into the Anlage of the olfactorius. The evidence given by many histologists, from Schulze to Retzius, establishes the ganglionic character of the olfactorius; while the evidence presented by His ('89^a) appears confirmatory of the view of Beard, that the olfactory plate is to be regarded as the anterior of the sense organs of the lateral line, since from it are derived, at least in part, the ganglionic cells of the olfactorius. Therefore, if neural-crest cells also entered into the Anlage of this nerve, it must be regarded as homodynamous with the sensor component of a dorsal segmental nerve.

2. Abducens.

Another of the eye-muscle nerves, viz. the abducens, is now (65 somites, 10 mm.) differentiated. (Compare Figs. 20 and 21 with Fig. 19.) The latter nerve has arisen as an outgrowth from neuroblast cells in the ventral horn of encephalomere VII, and its roots retain connection with this encephalomere until the latter disappears. Zimmermann ('91) stated incorrectly that its connection in Squalus is with the neural segment which corresponds with my encephalomere VI. Dohrn ('90^a) describes the nerve as having its origin from the neural tube opposite the otic capsule, and between nerves VII and IX. Its position in different Vertebrates seems inconstant. Some investigators (Orr, '87, Waters, '92, and Herrick, '92) have stated that in the forms studied by them it arises from the hindbrain neuromere corresponding with encephalomere IV of my figures. In the chick and swine I have found that its roots are in connection with encephalomere VI, whereas in Necturus its fibres may be traced from the musc. rectus posterior to a point behind the ear, and thus have, as I believe, their origin from a segment of the hindbrain corresponding with encephalomere VII. At least, in this form, as in Squalus, it appears as a post-otic nerve. Dohrn ('91) gave a careful account of the early stages of its development in embryos of various Selachii. He states that the nerve first appears at a stage corresponding with Balfour's stage L, arising by two roots which unite at a short distance from their point of exit from the ventral wall of the neural tube. In Mustelus the roots are more numerous than in the other forms examined, there being as many as six on each side of the brain. The roots are directed backward, as in the case of spinal nerves, but later form a network from which arises the stem of the nerve; this runs forward, parallel to the neural tube, toward van Wijhe's third somite. In later stages the nerve divides into two branches, one passing along the inner side of the somite, and the other along the outer side. At first the nerve root, which appears as a plasma outflow from the neural tube, is of the thickness of one, or at most two, medullary cells. Later the roots increase in thickness, apparently by the continued outgrowth of plasma from the neural tube, as well as by the migration of cells from the ventral horn of the medulla. The larger size and different staining qualities of the medullary cells enabled him to distinguish them from the mesodermal cells in their vicinity. Such (medullary) cells are often found with a part of the nucleus within and a part without the medullary wall. This outflow (migration) of medullary cells takes place also in later stages after the white substance has become quite thick on the side wall of the neural tube.[1]

My observations upon the development of the abducens differ from those of Dohrn, as in the case of the oculomotorius, inasmuch as I find the nerve to arise from axis cylinder processes of neuroblasts in the ventral horn of the medulla, and therefore to resemble in its mode of development that of a ventral spinal nerve, as stated by His ('89). At the earliest stage which I have been able to detect the abducens, it possesses but a single root, formed by the processes of several neuroblasts, as is represented in Figure J. The union of these takes place just outside the medullary wall, yet peripherally the nerve appears as a single process with deeply staining axis and a more lightly stained sheath. I find neither at this stage nor in later stages any convincing evidence of a migration of the neuroblast cells from the wall of the neural tube. In later stages of development sections show that *the nuclei seen along the course of the nerve are distinctly peripheral in relation to its fibres.* Even the phenomena presented in sections of embryos fixed with corrosive-sublimate acetic, such as are represented in Figures 62–65 (Plate 9), warrant in my judgment only the inference that the nuclei of the nerve are peripheral, as held by Miss Platt ('91). The darker appearance of the nuclei lying upon the nerve results more from the opaqueness of the nerve than from any peculiar staining properties of the nuclei. During development the number of roots in the nerve increases from one to three or four, the number being variable even upon the two sides of the same embryo. The method of development of the secondary roots is the same as that described for the primary one, viz. as processes from neuroblast cells in the ventral horn. By following the fibres of the roots in the wall of the brain, it is easily ascertained that the motor "nucleus" of the abducens is a very elongated one, as is known to be the case in higher Vertebrates (see Edinger, '96).

---

[1] Since Marshall ('81), van Wijhe ('82), and Miss Platt ('91) never saw the early stages of development of the abducens, it is unnecessary to restate their results in this connection.

The study of the development of the abducens is simpler than that of the oculomotorius, since the nerve never comes into relation with a ganglion, and thus resembles the primitive ventral nerves of Amphioxus more than do the ventral spinal nerves. The gradual extension of its fibres through the mesenchymatous tissue at the base of the medulla may therefore be easily followed. It is a matter of some morphological importance, in my opinion, that not all the nerve fibrils extend anteriorly toward the third somite (van Wijhe's), but that in later stages of development, e. g. in embryos with 78–80 somites (Plate **4**, Fig. 20), a nerve fibril is seen to pass from the posterior root of the nerve in a posterior direction toward the myotome of the sixth somite, which has at this stage, however, only a few rudimentary muscle fibres. Miss Platt ('91) likewise has mentioned the fact that this nerve also distributes fibres to mesoderm posterior to the third somite (musc. rectus posterior). In the abducens, therefore, we have to do with a post-otic ventral nerve,

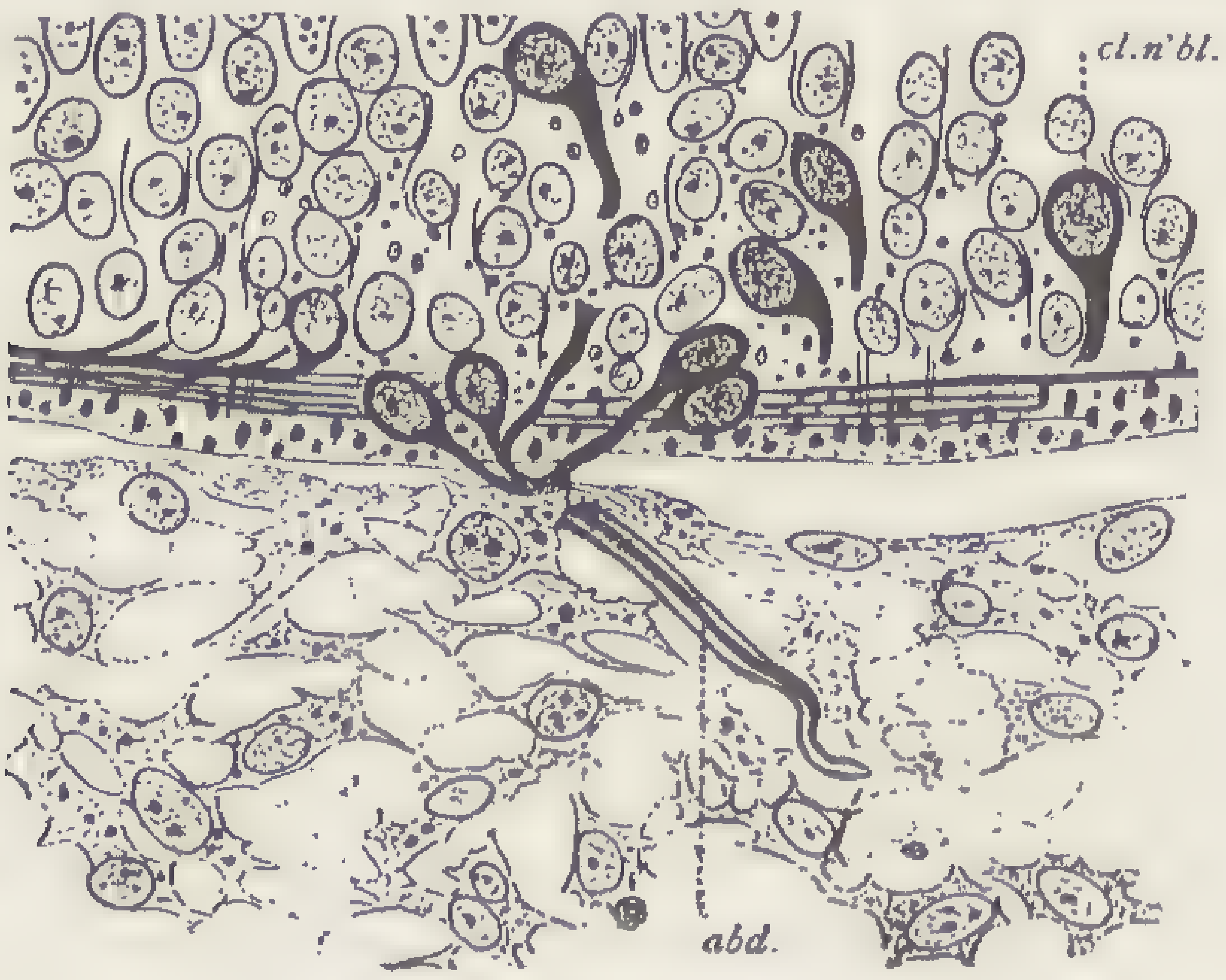


FIGURE J.

FIG. J. Parasagittal section of a Squalus embryo with 60 somites, showing the abducens as a fibril formed by the processes of at least four neuroblast cells. × 447. *abd.*, abducens; *cl. n'bl.*, neuroblast cell.

which develops in precisely the same way as do ventral (medullary) spinal nerves, possesses a much elongated motor nucleus in the ventral horn of the medulla, and innervates pre-otic (possibly also in the embryo post-otic) musculature (musc. rectus posterior). These facts seem significant in dealing with the question of the primitive metameric relations of this nerve.

At a stage when the embryo has a length of 17 mm. (78–80 somites) the ramus opthalmicus superficialis V (Plate **4**, Fig. 20; compare Fig. 21) appears as a fibrillar nerve with peripheral nuclei extending from the Gasserian ganglion just dorsal to the point of exit of the fibres of the r. ophth. profundus V, and passing anteriorly close to the ectoderm below the r. ophthalmicus superficialis VII. The relations of these two ophthalmic nerves are therefore such that they have usually been regarded as of the same morphological value, i. e. as rami cutanei dorsales of nerves V and VII respectively. Yet an interesting relation of protoplasmic processes from the r. ophth. sup. V with the myotome of the second somite, such as is represented in Plate **8**, Figure 60, has been called to my attention by Miss Platt. Since at this stage of development the fibres of the trochlearis have not appeared, the inference would seem warranted that motor impulses may have primitively passed to this myotome (musc. obliquus superior) through the fibres of the r. ophth. sup. V. Such a supposition, however, is greatly diminished in force, and in my opinion rendered untenable, by the fact that in embryos of 19 mm. — therefore before the fibres of the trochlearis are in connection with the m. obliquus superior — the r. ophth. sup. V shows no longer connection with this muscle (Figure K). The fibres of the anterior root (portio minor) of the trigeminus nerve may now be traced from their origin through the Gasserian ganglion into the mandibular arch, where they give off fibres both to the muscles of the arch and to the skin of its anterior and lateral surface. The fibres appear in large part motor. Since this is the only motor branch of the V, it would follow that the posterior root (portio major) includes chiefly, if not entirely, sensor fibres. It would moreover follow that encephalomere III is chiefly, if not wholly, connected with motor fibres, which may be traced forward to a considerable distance in it to the neuroblasts in the lateral horn, with which they are in connection, while encephalomere IV has chiefly sensory fibres in connection with it. Mitrophanow's ('93, p. 178) evidence is, however, considerably at variance with that just stated. He finds that in an embryo Squalus of 18 mm. "la racine du nerf trijumeau est large et se devise en deux parties (Pl. XIV. Fig. 8) dont les fibres sortent du cerveau en formant différents coins et se croisent ensuite au dedans du ganglion Gasseri; de cette manière le ramus ophthalmicus profundus les reçoit de la partie postérieure; le ramus maxillaris, de la postérieure et de l'antérieure; le ramus mandibularis, principalement de la postérieure." Mitrophanow's results are seen to differ markedly from mine as to the relationship of the fibres of the ramus mandibularis. My results, however, agree with those of His ('88^b, p. 365, Tab. II, Fig. 3) for the human embryo. The clear relationship of the motor fibres of the trigeminus with encephalomere III and the visceral part of van Wijhe's second cavity appears to me a matter of considerable morphological importance, and seems to establish the metameric relations of these elements.

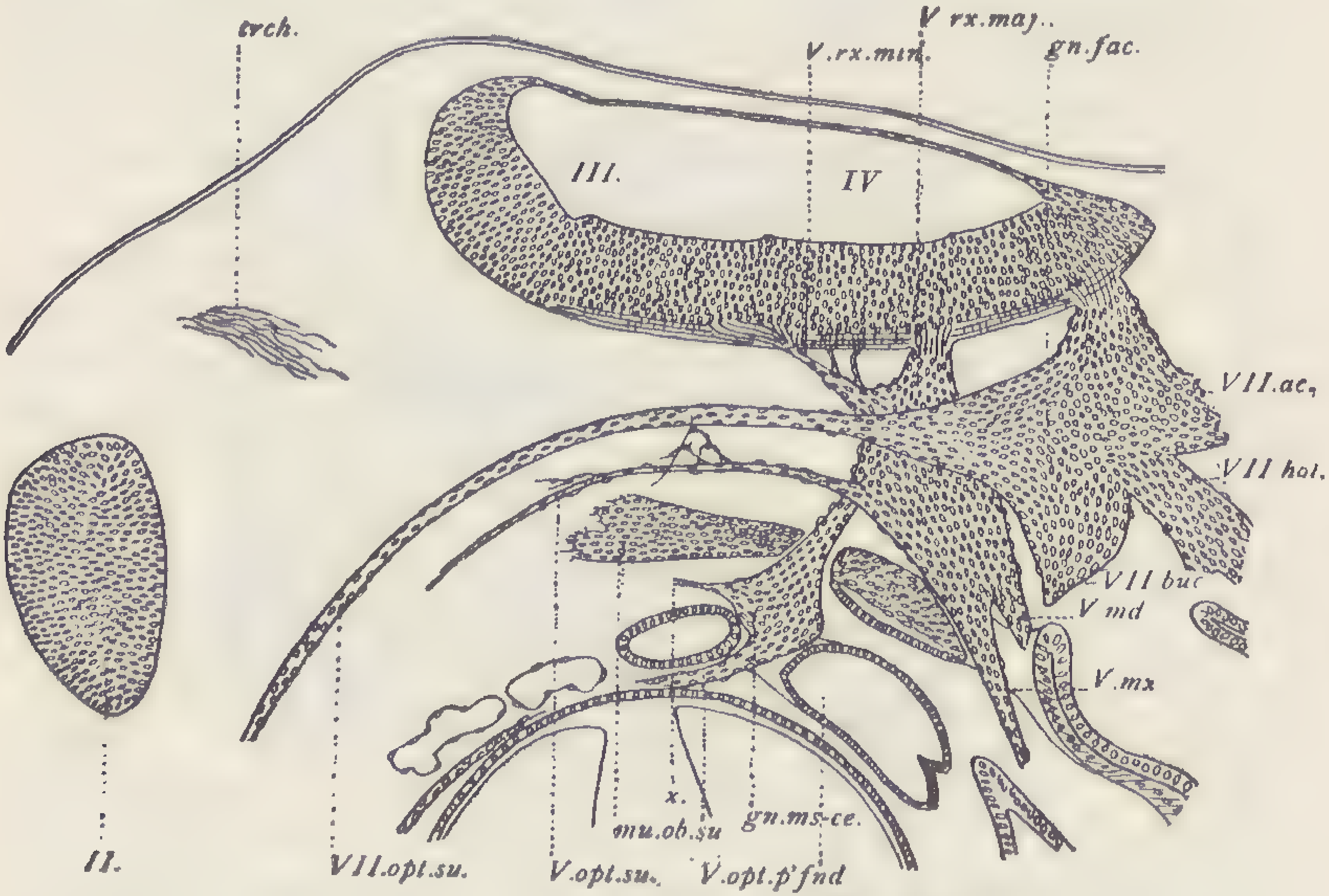


FIGURE K.

FIG. K. Parasagittal section through the left side of a Squalus embryo of 19–20 mm. × 50.

II, III, IV, second, third, and fourth encephalomeres; *V. md.*, r. mandibularis trig.; *V. mx.*, r. maxillaris trig.; *V. opt. p'fnd.*, r. ophth. profundus trig.; *V. opt. su.*, r. ophth. superficialis trig.; *V. rx. maj.* and *V. rx. min.*, major and minor roots of the trigeminus; *VII. ac.*, r. acustico-facialis; *VII. buc.*, r. buccalis facialis; *VII. hoi.*, r. hyoideus facialis; *VII. opt. su.*, r. ophth. superficialis facialis; *gn. fac.*, ganglion of the facialis nerve; *gn. ms-ce.*, meso-cephalic ganglion still retaining connection with the ectoderm by the process *x*; *mu. ob. su.*, m. obliquus superior; *mu. rt. su.* + *a.*, musc. recti superior and anterior (1st cavity); *trch.*, trochlearis.

3. TROCHLEARIS.

In an embryo about 21–22 mm. in length (Plate **4**, Fig. 21) the trochlearis, the last cranial nerve differentiated, appears, as stated by Kastschenko ('88, p. 465), in the form of "parallel gehende kernlose und, dem Anschein wenigstens nach, vollständig structurlose Fäden, welche in ihrer ganzen Ausdehnung vom Gehirndach bis zum entsprechenden Muskel verfolgt werden können." The great variety of opinions concerning the morphology of this eye-muscle nerve make interesting the facts of its development. Hoffmann ('89, p. 338), who was the first to study its development, states that in Lacerta one finds, as the Anlage of the trochlearis, "einen ziemlich grossen, zelligen Auswuchs" between midbrain and hindbrain. At certain stages the trochlearis possesses "ein sehr deutliches und zwar ziemlich grosses Ganglion, welches aber frühzeitig wieder vollständig abortirt."[1] In later stages of development the trochlear emerges as "dünner, feinfaseriger Nervenstamm von der oben erwähnten Stelle aus dem Gehirn und wird in seinem weiteren Verlauf bald so schmächtig, dass er nur aus einzelnen, sehr dünnen Fasern besteht." In other reptiles, in birds, and in cartilaginous fishes, Hoffmann was unable to find evidence of this ganglion of the trochlearis. In 1890 and 1891 Dohrn announced that, in early stages of the development of the trochlearis, erratic ganglia, which were evidently products of the neural crest, are found in Selachian embryos in connection with this nerve. Whether these ganglia send fibres into the trochlearis stem, he was not able to determine. In later stages anastomosing fibres appear to connect the trochlearis with the r. ophth. sup. V and VII. Moreover, Froriep ('91) thinks he is able to establish in Torpedo the genetic connection of a pear-shaped ganglion with the trochlearis. From his studies upon Torpedo embryos, he is also forced to conclude that the trochlearis arises *in situ* through the "Umwandlung oder Ausläuferbildung der Ganglienzellen." According to Miss Platt ('91, p. 95), the trochlearis in Acanthias first appears as a small fibrous nerve growing from the constriction between midbrain and hindbrain. This may be followed a short distance into the mesoderm, but, becoming extremely attenuated, is soon lost. "Soon after the appearance of this small nerve, which is the root of the permanent trochlearis,[2] cells are proliferated to meet it from the ganglion cells that lie above the superior oblique muscle. Thus the permanent trochlearis arises from two sources, from the brain and from ganglion cells." Finally, Kupffer ('91) stated that he had found a nerve in Ammocœtes, which he thought to be the trochlearis (for reasons not clear to me), directly connected with the second epibranchial ganglion. Were this opinion correct, the trochlearis would be the serial homologue of a branchial (dorsal), not of a spinal dorsal nerve.

---

[1] Confirmed by Oppel, '90.

[2] Miss Platt makes, in my opinion, an unnecessary distinction between a "primary" and a secondary, or "permanent" trochlearis. The "primary trochlearis"

From this summary of previous embryological evidence bearing on the question of the morphology of the trochlear nerve, it is clear that little support is given to the view, based on the later histological structure and relations, that it is morphologically a ventral segmental nerve. Only Kastschenko ('88) finds the nerve in early stages fibrillar in structure. The following evidence, however, leads me to conclude that its mode of development is the same as that of the oculomotorius and abducens, and that therefore it must be regarded, like these, as a ventral (medullary) nerve. I first find the trochlearis in sections of embryos of 19–20 mm. as a fibrillar nerve bundle extending from the dorsal constriction between encephalomeres II and III. Two roots are already present at this stage, but neither in these, nor in the nerve bundle as far as its fibres may be traced in the mesenchymatous tissue at the sides of the brain, are nuclei to be found. While proximally the nerve fibres are united in a compact bundle, they distally separate so as to form a loose brush of structureless fibres, which are lost in the mesenchyma at a considerable distance dorsal to the musc. obliquus superior (Figure K). While I am able to offer no direct evidence in favor of the view that the fibres of the trochlearis, as above described, are processes from neuroblast cells in the ventral horn of encephalomere III, I hold that they are such, since their well known later histological relations support this conclusion. Dorso-ventral fibres in this region of the neural tube may indeed be traced in embryos of this stage, but their connection with the fibres of the trochlearis is not clear to me. The dorsal chiasma of fibres is present.[1] Of a ganglion, or of any grouping of cells which might

---

is that portion of the trigeminus Anlage which I have for convenience called its trochlear portion, which persists for some time in the constriction between midbrain and hindbrain vesicles. Since the proof of its morphological value has not been given, and since the "permanent" trochlearis is not developed from the "primary" trochlearis, as Miss Platt herself states (p. 96), the use of the latter term appears to me apt to mislead.

[1] The explanation for this dorsal chiasma may be sought in some physiological advantage in coördination gained, but it may also be seen that in case the dorsal exit of fibres were of physiological advantage, it would be easy for the fibres to

receive the name of ganglion, there is no evidence at this or later stages. The last traces of scattered groups of neural-crest cells found in some (not all) embryos of earlier stages (17 mm.) have been lost.

In embryos of 21 mm. some of the distal fibrils of the nerve appear to have united with migratory cells from the r. ophth. sup. trigeminus, a process in my opinion comparable with that which takes place in the growth of the oculomotorius. At least, in embryos of 21 or 22 mm. the distal portion shows nuclei in relation with the nerve fibres, whereas proximally no nuclei are seen. In still later stages the nerve has a distinctly cellular appearance throughout its length. The nuclei are, however, seen in thin sections to be peripheral in relation to the nerve fibres, as in the oculomotorius (Figure I). The evidence of anastomosis of the fibres of the trochlearis and the r. ophth. sup. trigemini I consider very doubtful. During development the loose brush of fibres at the distal termination of the trochlearis becomes united into a compact nerve stem. It has, therefore, seemed to me that the primary widely spread brush of nerve fibrils may be explained on the ground of advantage gained in seeking the terminal organ, the musc. obliqu. superior.

The phenomena observed by me during the development of the trochlearis are seen to correspond very closely with those observed by Miss Platt ('91). To her, as to me, the trochlearis first appears as a fibrillar process from the dorsal wall of the brain. But while she interprets the evidence of cellular growth toward the advancing end of the nerve as of morphological or phylogenetic significance, I am unwilling to give it such interpretation, since I find that these nuclei have nothing to do with the nerve proper. In my opinion, it is probable that they become converted into the nuclei of Schwann's sheath, an opinion which seems confirmed by their peripheral position in relation to the nerve fibres. When the only sections I possessed were of embryos killed with corrosive-sublimate acetic, and stained with carmine or hæmatoxylin, the evidence seemed to me confirmatory of the view of Froriep ('91), viz. that the trochlearis is differentiated from mesenchymatous cells *in situ*. But better methods of preparation have taught me to distrust that evidence, and the results appeared to me too distinctly contradictory to the later histological

---

cross each other in growth, since the direction of their growth would thereby be unchanged. I assume that it is easier for a nerve fibre to grow in a direct line than to bend back and reverse the direction of its growth. The *possibility* even of a primary connection of muscle and nerve appears to me to be excluded in the case of the musc. obliq. sup. and the trochlearis.

structure of the trochlearis to be worthy of trust, or even of serious consideration.

Before closing my account of the development of the cranial nerves and their chief branches in Squalus, I wish to call attention to a phenomenon seen in still later stages of development, already noted by me in a former paper ('97, p. 455). It appears to me a matter of considerable morphological importance that the ganglion of the dorsal nerve of van Wijhe's eighth somite (fourth post-otic) — the ventral root of which forms at this stage the first of the five hypoglossus roots — unites in late stages of development with the ganglion cells near the root of the vagus. Kupffer ('90) was the first to make evident the morphological importance of the clearly marked distinction between dorsal and lateral (epibranchial) ganglia in embryos of Cyclostomata. While in the embryos of Selachii there is not such a clearly marked distinction, there nevertheless exist at the roots of the vagus groupings of ganglion cells, or at least of neural-crest cells (quite distinct from the lateral, epibranchial ganglia of this nerve, the ganglion nodosum), which in my opinion are to be regarded as homologous with the dorsal ganglion of the vagus of Ammocœtes.[1] The evidence of the union of dorsal segmental ganglia in the vagus is as follows. During development the continuous neural crest in the occipital and trunk regions of Squalus becomes differentiated into clearly marked ganglia, lying opposite the myotomes and connected by a cellular "dorsal commissure" (Balfour, '81), as far forward in the embryo as van Wijhe's seventh somite. Opposite the sixth and seventh somites no distinct ganglia appear; but instead a wide sheet of cells, lying in close juxtaposition to the extended roots of the nerve, is observable. While in early stages the ganglion of the eighth somite is separated by a considerable interval from the roots of the vagus, in later stages it approaches these, and in embryos of 30 mm. is seen to be in union with them as a well marked ganglionic appendage. In later stages, its fusion appears complete. The ganglion cells do not degenerate, but send axis-cylinder processes both centripetally and centrifugally, the latter forming the posterior of the *roots* of the vagus nerve. The ganglion of the second hypoglossus root (ninth somite) does not, however, so fuse with the vagus, but is seen in embryos of 50 mm. as a group of cells without nerve relations, so far as I am able to determine, enclosed in the cartilage of the cranium. It apparently disappears in later stages, as does its ventral root, the hypoglossus of the adult having, according to Gegenbaur ('72) and M. Fürbringer (97), only two ventral roots without dorsal ganglia. Since the reduction of dorsal and ventral roots takes place from the anterior towards the posterior, these two ventral roots of the adult hypoglossus are in all probability the posterior of the five roots of the embryo.[1] A similar process of fusion of dorsal ganglia with the dorsal ganglion of the vagus takes place in Petromyzon; but in that animal the fusion of the ganglion — viz. that of the "spinalartige Vagusanhang," which for reasons already stated by me ('97, pp. 454, 455) I regard as the exact homologue of the dorsal ganglion of van Wijhe's eighth somite in Squalus[2] — appears by a comparison of the results of Wiedersheim ('80), Schneider ('80), Ahlborn ('84^a), Hatschek ('92), Kupffer ('96), and M. Fürbringer ('97) to be a variable one. This union of dorsal spinal ganglia with the ganglion of the vagus, taken in connection with the fact previously stated by me ('97, p. 453), that the dorsal ganglia of the glossopharyngeus and vagus lie *primitively*[3] median to the dorsal portion of post-otic somites, is a further link in the chain of evidence which shows that no fundamental distinction between spinal and cranial nerves exists. From the foregoing account it will be seen that, as in the case of spinal nerves, we are able, using as criteria the central and peripheral relationships of the motor fibres, to divide cranial *motor* nerves (roots) into two classes, viz.: (1) dorsal (splanchnic) roots, having their nucleus in the lateral horn of the neural tube and their peripheral distribution in the musculature (ventral) of the visceral arches; and (2) ventral (somatic) roots, which have their nucleus in the ventral horn of the neural tube and their peripheral distribution in the musculature (dorsal) of the somites (somatic musculature). The motor fibres of nerves V, VII, IX, and X belong to the former, and nerves III, IV, and VI to the latter class.

---

[1] These are probably the homologues of the intracranial ganglia of Ganoids (see Allis, '97, p. 747).

---

[1] Hexanchus and Heptanchus both have *five* hypoglossus roots in the *adult* (M. Fürbringer, '97).

[2] Homologized, however, by Ahlborn ('84^a) with van Wijhe's tenth somite, and by Hatschek ('92) with van Wijhe's seventh somite.

[3] Goronowitsch ('92) first observed in the chick that the topographic relation of the vagus to the head somites is the same as that of the spinal nerves to the trunk somites. Sewertzoff ('95, p. 92) also states that "Die Beziehung der Kopfmyotome zu den Kopfnerven, z. B. zum N. vagus ist dieselbe, wie diejenige zwischen den Rumpfmyotomen und Rückenmarknerven, d. h. sie liegen nach aussen von Nerv (Cyclostomata, Ganoidei chondrostei, Urodela, Reptilia, Aves)." This is stated, however, by Kupffer ('94, '96) not to be a *primitive* relation of the post-otic myotomes in Petromyzon. My own observations and conclusions, however, differ from those of Kupffer (see Neal, '97, p. 453). Miss Platt's ('97) observations on Necturus, and her conclusions likewise, confirm the conclusions of Goronowitsch and Sewertzoff.

While it is possible, as has been stated, to establish a numerical correspondence of encephalomeres and somites, the nerve relations are not so clear. We find, for example, that encephalomeres II, III, and VII are connected by ventral (motor) nerves with somites (van Wijhe's) 1, 2, and 3. Such evidence of a want of segmental correspondence would seem at first sight to render untenable the assumption that encephalomeres have the same segmental value as myelomeres. We have already seen that these two classes of neuromeres have structurally little in common. Moreover, a want of correspondence of encephalomeres and visceral arches is shown by the fact that the *dorsal* motor fibres which are connected with encephalomeres III and V innervate two *successive* visceral arches. In view of this discrepancy in the segmental relations of encephalomeres and nerves, can we regard the former of segmental value? Do they afford evidence in support of the assumption that a Vertebrate head segment is comparable, i. e. homologous, with a trunk segment? Before expressing my own opinion in regard to the answer to this question I will briefly review the interpretations given by previous investigators. Two antithetic views concerning the neuromeres have been given, viz. (1) that they are not of segmental or phylogenetic value, and (2) that they are of phylogenetic value.

VII. Segmental Value of Hindbrain Neuromeres.

a. Non-phylogenetic Interpretation.

In 1877 Mihalkovics, speaking of the foldings in the medulla of birds and mammals, expressed the opinion that the want of correlation between these structures and the nerves and visceral arches seems to favor the view that they are of mechanical origin, i. e. formed by the bending and shoving of the neural tube as it rapidly grows in a confined space. This view seems strengthened by the consideration that the ventral wall of the neural tube of chick embryos is, in early stages, markedly folded into segments, irregular in size and inconstant in appearance, and that these folds in the head region are visibly exaggerated by certain fixing agents which result in shrinking the embryo. Balfour, who with Foster ('74) had been the first to express the opinion that these structures were of phylogenetic significance, afterwards ('81) said that it is uncertain whether they have any morphological significance. In 1892

Froriep, in speaking of neuromeres and their nerve relations, said that these relations are in no way of such a kind that both nerves and neuromeres appear to be constituent parts of a simple organ system. The nerves, especially the trigeminus and facialis, are not so constant in their relation to the folds as would be expected, if the latter were primary segments of the nervous system. It looks much more as if the presence and position of the nerves determines the position of the folds, and as if the appearance of the folds is itself a passive, mechanical one, necessitated by quick growth in length in a confined space. On the basis of his research, he was therefore much inclined to consider these late appearing and transitory segments of the brain as morphologically unimportant phenomena.

Broman ('95) has given a somewhat extended description of the foldings in the hindbrain of a human embryo about three weeks old. Although he nowhere formulates his conclusions as to the significance of the folds, it is evident that he does not regard them as of phylogenetic significance, for he says that the correspondence which earlier investigators have found in their relation to nerves seem to him of little help. In his opinion the results, differ too much to allow one to think that a general rule prevails in the Vertebrate series as regards the number and relations of the foldings. The foldings, he says, are intensified in the regions of the greatest flexure of the neural tube, and in these regions the radial arrangements of cells in the foldings is also more marked. This, together with the fact that the foldings are confined to the ventral half of the medulla, harmonizes well with a mechanical explanation of their origin. Upon the evidence that rounded cells (which he thinks are the neuroblasts) with round nuclei may be distinguished in the centre of the most strongly developed parts of the brain foldings, Broman ('95, p. 189) forms an hypothesis concerning the origin of the separation of lateral and ventral roots. He says: "Wenn wir noch einmal alle die oben von mir als Neuromeren bestimmten Falten durchmustern, finden wir, dass nur das als Abducensneuromer bezeichnete die ventrale Wand des Hirnrohres ausbaucht. Alle übrigen sind entweder ganz und gar davon abgedrängt, oder auf dem Wege es zu werden. Dies kann natürlicher Weise ein blosser Zufall bei diesem Embryo sein."

Since Broman's paper is, with the exception of Locy's, the most recent one on the question of neuromeres, I will discuss his evidence and conclusions at some length. It is unfortunate for the purpose of discussion that he has failed to identify correctly the cerebellum Anlage. What he calls Cerebellumanlage is the posterior of the two secondary subdivisions of encephalomere III, as may easily be determined by a comparison of his figures with frontal sections of swine embryos. He says (p. 188), "Die ventrale Ausbuchtung der zweiten Falte kann man also mit vollkommene Sicherheit für die beginnende Ponsanlage, und ihren oberen Theil für die Cerebellumanlage halten." But, as may be determined by the relations of the neuromeres to the ear capsule and to the ganglia of the acustico-facialis and the trigeminus in his figures (Taf. X. Figs. 4, 5), the true Anlage of the cerebellum lies anterior to this and is his "erste Falte," which on theoretical grounds he considers related to the trochlearis nerve. As a result of this mistake it happens that the neuromere which he calls "Abducensneuromer" (VI), and to which on purely theoretical grounds he assigns the sixth nerve, is in reality encephalomere V, which is connected with the acustico-facialis. *With this neuromere the abducens never is connected in any Vertebrate yet studied.* In the swine, as I am able to affirm from my own observations, the abducens arises from the ventral portion of hindbrain neuromere VI, which in the early stages of all Vertebrates lies opposite the ear capsule. In Necturus, the chick, and S. acanthias, its origin is ventral and posterior to the origin of the acustico-facialis. In support of this theory of the mechanical origin of the "Falten," Broman finds that, as a result, as he thinks, of the flexure of the neural tube, those neuromeres which correspond with encephalomeres IV and VI of my figures are wedge-shaped, and that their ventral edges do not reach the ventral wall of the neural tube. Moreover, none of his neuromeres extend to the "Deckplatte." But a study of swine embryos leads me to conclude that this is not characteristic of all mammalian embryos, and indeed that it may be "ein blosser Zufall" in the case of Broman's human embryo. In young swine embryos (killed 19 days after coitus) *none of the neuromeres are wedge-shaped ventrally or dorsally;* moreover, the constrictions between them extend into the Deckplatte. The posterior constriction of encephalomere V extends *across* the Deckplatte until a somewhat later stage, and in this constriction a mass of neural-crest cells persists in a way precisely similar to that in which neural-crest cells in S. acanthias persist in the regions of constriction between the primary brain vesicles (encephalomeres).[1]

From an examination of the evidence presented by those who have held that the neuromeres are purely the result of mechanical influences, it is evident that the chief support for the hypothesis consists, first, in an apparent want of a definite relation of the nerves to the neuromeres in the different Vertebrate groups, — i. e. an apparent inconstancy in the structures themselves, — and, secondly, in the fact that the hypothesis seems to explain the structural conditions presented.

---

[1] In connection with this fact, it is to be noted that the walls of the medulla in this region are little distended laterally, which may be ascribed to the influence of the ear capsule. (See Plate 5, Fig. 30.)

I turn now to a consideration of the arguments supporting the view that the neuromeres are of morphological (phylogenetic) importance.

b. Phylogenetic Interpretation.

A phylogenetic interpretation of the foldings of the medulla was first given in 1874 by Foster and Balfour. The following year Dohrn accepted this explanation. Béraneck ('84) showed that in the Lizard the hindbrain folds ("replis") were definitely related to certain nerves. Having later ('87) confirmed his observations by studies of chick embryos, he concluded that the foldings are *the last indisputable remnants of the primitive segmentation of the head.* It is notable that he reached this conclusion notwithstanding the fact that, in his opinion, the segments of the spinal cord do not have the same characters as those found in the foldings of the hindbrain. Subsequent investigators, however, have sought to compare encephalomeres with myelomeres. In 1885 Rabl found in chick embryos a regular folding of the side walls of the myelencephalon, the segments of which showed the same characteristics as the foldings in the region of the spinal cord. During the same year Kupffer ('86), in studies on different Vertebrate embryos, found that the foldings extended into the midbrain region. Because of the relatively late appearance of the folds, — "after the closure of the neural tube, after the formation of three brain vesicles, and long after the segmentation of the mesoderm," — Kupffer thought that there was much against the interpretation of these folds as remnants of a primary general metamerism of the neural tube, but his later observations — previously cited in another connection (p. 174) on an embryo of Salamandra atra at a stage before the closure of the neural plate — led him to believe that in this particular case there is a primary segmentation.

The fact that Kupffer here found eight cross furrows in the brain region, representing as many "ancestral segments," appears to have strongly influenced his subsequent interpretations of the morphology of the forebrain in different Vertebrates, for in his later studies he has sought to find evidence of these eight primary "encephalomeres" in the forebrain and midbrain, *even* "after the closure of the neural tube, and the formation of the three brain vesicles, and long after the segmentation of the mesoderm"!

McClure ('89, p. 435, and '90, p. 37) concluded, from studies on embryos of Amblystoma, Anolis, and chick, "that the symmetrical constrictions or folds found in the lateral walls of the embryonic brain are remains of the primitive segmentation of the neural tube, in part atavistic, extending [from the spinal cord region] into the primary forebrain." The serial homology of the segments of the myelon and the encephalon seemed to him certain, since he found both the structural characteristics and the nerve relations to be the same in the two regions. "The dorsal roots of spinal nerves take their origin from the *apex* of their respective myelomeres in exactly the same manner as the nerves of the medulla do from their respective encephalomeres" ('89, p. 437).

In the same year Miss Platt ('89) also advocated the view that there is a serial homology between the encephalomeres and the segments of the spinal cord. While she agrees with Orr and Béraneck in regard to the number and appearance of the neuromeres and the ultimate relations of the nerves, she finds that the cranial nerves develop from the *constrictions* between neuromeres, precisely as the spinal nerves do. In answer to objections to the attempted homology between cranial and spinal segments, she says that in both head and trunk the segmentation is transitory, and that in both regions it is more manifest in the ventral portion of the neural tube.

The conclusions of Waters ('91) are largely confirmatory of those of McClure, viz. that there is a similar segmentation in brain and spinal cord, with similar sensor nerve relations in both these regions.

Zimmermann ('91), as a result of his studies on rabbit, chick, and Squalus embryos, thinks he is able to confirm Kupffer's discovery of eight primary cephalic segments or "encephalomeres," although his eight "primäre Abschnitte" include forebrain, midbrain, and hindbrain regions, while Kupffer's theoretical conclusion was that his eight "primäre Medullarfalten" do not include the hindbrain.[1] Although Zimmermann states that the spinal cord does not appear segmented, he finds in later stages thirteen homodynamous "encephalomeres," and has given a table of these with their nerve relations. He supposes three roots, a dorsal, a lateral, and a ventral one, to be related to each encephalomere, but his table gives chiefly the impression of numerous gaps to be filled with hypothetical nerve roots.

Herrick ('92) states that he finds the segmentation of the medulla

---

[1] At first Kupffer thought they did not include the forebrain!

and spinal cord of snake embryos not explicable on mechanical grounds. "The neuromeres of the medulla cannot be ascribed to the mechanical influence of the Anlagen of the nerves, for those segments which have no nerves develop equally with the others" (cf. Froriep, '91). He considers however "the neuromeres of the forebrain" region wholly illusory from a morphological standpoint, since they involve only dorsal structures.

c. Interpretation of Hindbrain Neuromeres in Squalus acanthias.

I believe that the evidence which I have obtained from a study of the development of hindbrain neuromeres in S. acanthias excludes the possibility of a simple mechanical explanation of them. In their earlier stages they were seen to be local thickenings of the lateral walls, a phenomenon intelligible only on the ground of unequal growth, and not in the least explicable as the result of the passive bending or shoving of a tube already formed.[1] Since the somites do not extend into the region of the dorsal part of the encephalomeres, the possibility that the neural tube in this region is constricted by them is excluded. They are, then, in both structure and mode of development, clearly not to be explained in the same way as the myelomeres. Again, that they are not due to the effect of the Anlagen of the nerves, as supposed by Froriep, is shown by the fact that encephalomere IV develops equally with the others, although there is no nerve in relation with it until a comparatively late stage. Since the fibrillar connection of nerves with neuromeres is established almost at the same time that the inner surface of the hindbrain neuromeres becomes concave, it might be thought that this change is due to the mechanical effect of nerve fibres. That such is not the case seems clear, however, because no nerve fibres come into relation with the outer convexity of encephalomere VI. The hindbrain neuromeres, from their early appearance onwards until they disappear, are local differentations of the walls of the medulla, and as such are not, I believe, to be satisfactorily explained on simple mechanical grounds. On the other hand, I hold that they do possess certain characteristics which admit of a mechanical explanation. This seems to be supported by evidence from two sources. In the first place, a fixing agent which causes a contraction of the tissues of the embryo intensifies the constrictions between the neuromeres. By this means the radial arrangement of cells and nuclei is still more sharply emphasized. I think we may safely assume that this effect is the same as that resulting from a shoving of the neural tube due to rapid growth in a confined space. Figure 28 (Plate **5**) shows a frontal section of a preparation of a shark embryo, nearly 10 mm. long. The specimen was fixed in the mixture of picrosulphuric and chromic acids, and then transferred directly to 50 per cent alcohol. Inadequate fixation and immediate transference to a fluid of very different osmotic power resulted in a strong contraction of the embryo, particularly emphasized in the wall of the neural tube. (In the figure the constrictions appear exaggerated, since only the regions of the nuclei are shaded.) Moreover, a comparison of embryos of different Vertebrates gives evidence, as it seems to me, that the bending of the neural tube results in the intensification of the characteristics of neuromeres. I have studied in frontal section embryos of Petromyzon, Gadus, Amblystoma, S. acanthias, chick, and swine. The radial arrangement of cells is more pronounced in those forms which have a stronger flexure, and in which, therefore, we may safely assume that there is a greater shoving of the neural tube, due to rapid growth in a confined space. These characteristics are considerably more pronounced in Sauropsida than in S. acanthias, in which the flexure of the neural tube is, however, considerable. This explanation tends to remove the doubt as to the phylogenetic value of such structures as the neuromeres which naturally arises when these are shown to be structures slightly if at all visible in the lowest Vertebrates (Amphioxus and Cyclostomes), while well marked in the highest. I believe that the presence of yolk makes the conditions in both Petromyzon and Amblystoma less primitive than in Squalus, chick, and swine.

---

[1] This is true also in swine and chick embryos; but I do not find in Amblystoma as good evidence that the neuromeres are local thickenings of the neural wall.

In Gadus and Amblystoma the radial arrangement of cells and nuclei is even less pronounced than in S. acanthias, and this seems to be correlated with the fact that the flexure of the neural tube in the former is less marked than in the latter. It must be admitted, however, that the presence of much yolk in the cells of the neural tube of Amblystoma (Plate **5**, Fig. 35), in which no sign of encephalomere IV is present, may be concerned in producing the different condition of this form, in which the outpocketing of the neural tube takes place in the region of the proliferations of the ganglionic Anlagen only. Broman ('95, p. 186) has given proof, satisfactory as it seems to me, that the nuclear and cellular characteristics of the neuromeres of the human embryo may be explained partly on mechanical grounds. Embryologists are agreed that the flexures of the neural tube may be accounted for by the rapid growth of the tube in a confined space. Such growth would clearly result in a shoving of the neural tube, and also in a flexure in weaker portions, as in the regions between local thickenings, like the hindbrain neuromeres. The crowding of the cells in the regions of constriction between neuromeres may be accounted for in the same way. I therefore conclude that *some* of the structural characteristics of neuromeres may be intensified by the bending or shoving of the neural tube during its growth.

The conditions presented in Amblystoma (Plate **5**, Fig. 35) led me to believe at one time that the neuromeres might be related to the proliferation of the cells of the ganglionic Anlage. In this animal the neural tube is evaginated in the regions of the proliferation of cells for the ganglionic Anlagen of nerves V, VII, IX, and X, while in the region where no neural-crest cells are proliferated — the region corresponding to the position of encephalomere IV (in other forms) — no neuromere appears.[1] In S. acanthias we have seen (page 215) that from two of the hindbrain neuromeres, viz. V and VI, are proliferated the cells of two distinct nerve Anlagen. But since no nerve Anlage is proliferated from encephalomere IV, although this is as well marked as other encephalomeres, I was compelled to abandon the hypothesis, to which the study of Amblystoma had inclined me. *The fact that particular nerve Anlagen are proliferated from particular encephalomeres may, however, be a clue to the primitive mutual relationships of these nerves and of the encephalomeres to each other.* The fact that the local thickenings are confined to that region of the neural tube from which the great nerves of the head — V, VI, VII, IX, and X — arise, must also give us some clue as to their significance. Such local thickenings are seen neither in the region anterior, nor in that posterior to the medulla, but they are not limited by the ear capsule posteriorly, and the anterior boundary of them does not coincide with the anterior boundary of the primary hindbrain vesicle. It is to their nerve relations, then, that an investigator must first turn his attention. We have seen that in the development of the neural crest some of the cells of the trigeminus are proliferated from encephalomere III; that few cells are proliferated from encephalomere IV; that from encephalomere V come the cells of the acustico-facialis, from encephalomere VI the cells of the glossopharyngeus, and from encephalomere VII the cells of the Urvagus. The clearly marked relations of the Anlagen of the two suc-

---

[1] The migration of cells from certain regions of the neural tube would certainly weaken these regions, and the tube would in consequence, if subjected to a longitudinal pressure, or to distention by growth, tend to bend or distend most readily in such places.

cessive nerves, the facialis and the glossopharyngeus, to two successive encephalomeres (V and VI), seems to me to be a very important fact.[1] The cells of the glossopharyngeus are crowded back by the ear capsule, but the fact that in their ventral course they are directed anteriorly into the third visceral arch goes to prove that their posterior position is not their primitive one. Almost as clear is the relation of the cells proliferated from encephalomere VII to the second branchial (4th visceral) arch. From these facts I was led to think that the primitive relations of the hindbrain neuromeres were with the visceral arches. The fact that the hindbrain neuromeres are local thickenings of the lateral walls of the medulla also leads to the opinion that they are segmental groupings of the "Kerne"[2] of the nerves of the visceral arches. With this hypothesis in mind, I have examined the evidence in S. acanthias, as well as in other forms, in order to see if the facts support it. The more primitive relations would be expected to occur in S. acanthias. From encephalomere III are proliferated neural-crest cells which enter the mandibular arch; later this encephalomere becomes related with the motor root which innervates the muscles of this (mandibular) arch. Its relations, then, are clearly with the first visceral arch, and we may therefore assume that its local thickening contains, at least in part, the "nucleus" of the trigeminus.

The evidence obtained from the study of the relations of encephalomere IV seems at first sight strongly against the hypothesis. Few cells are proliferated from this neuromere. Late in its development the fibres of the sensor root of the trigeminus connect with its convexity. It forms a marked exception in its nerve relations to the other hindbrain neuromeres. Were it not that other facts are found which serve to bring this apparent exception into harmony with the hypothesis, the adverse evidence it presents would seem an insurmountable obstacle to the acceptance of my view. Neural-crest cells which pass into the second visceral (the hyoid) arch are proliferated from hindbrain neuromere V, and the motor fibres in relation with this neuromere innervate the muscles of this arch. From hindbrain neuromere VI are proliferated the neural-crest cells which pass into the third visceral (1st branchial) arch, and the motor fibres of the glossopharyngeus, of which these cells form the ganglionic Anlage, innervate its musculature. The place of origin of the fibres of the glossopharyngeus is crowded backward, evidently by the growth of the ear capsule. The place of origin of the roots of this nerve are variable. In swine and chick, for example, they have their origin from encephalomere VII, while in S. acanthias they arise behind this encephalomere. This is correlated with the fact that the ear capsule in S. acanthias is crowded backward into the region opposite encephalomere VII, whereas in the swine and chick the ear capsule continues to lie opposite encephalomere VI until long after the nerve assumes fibrillar connections with the neural tube. We may thus explain the variation in the position of the roots of this nerve, and still believe from the evidence that their primitive relations were with encephalomere VI.

---

[1] Hoffmann ('94) has spoken of the paired segmental outpocketings of the neural tube of this region.

[2] That is, they may be localizations of the motor "Kerne" and of the sensor "Endkerne" of the nerves primitively related to them.

Again, the cells proliferated from encephalomere VII are those which pass into the fourth visceral (2d branchial) arch, and form the Anlage of the Urvagus, whose motor fibres innervate the musculature of that arch. The Urvagus assumes fibrillar connections with the neural tube at a point behind the origin of the glossopharyngeus, and the cause of this change of relation may safely be assumed to be the same as in the case of that nerve. We have good evidence, then, that the primitive relationships of four of the hindbrain neuromeres were with the first four visceral arches. This relationship consists chiefly, but not wholly, in the fact that from these four neuromeres are proliferated cells which enter these arches and there form, in part at least,[1] the ganglionic Anlagen of the nerves related with them. The origin of these cells from the neural crest would naturally lead us to infer that in dealing with them as nerve Anlagen we are not dealing with motor nerves. We are, however, really dealing with the Anlagen of nerves which later become mixed. But in later stages, when the nerve roots are established, the roots of only two of the nerves in question, viz. V and VII, have their exit from the encephalomeres from which their ganglionic Anlagen arose. Have we a right, then, to assume that the exits of the roots of the other two nerves, IX and X (Urvagus), have been pushed back from the position which may be assumed, on the evidence of the relations of their ganglionic Anlagen, to have been the primitive one? I believe that we have, because, as we have seen from the examination of the relations of the roots of these two nerves, these roots lie as close to the point of origin of their ganglionic Anlagen as the ear capsule will permit. In a form like S. acanthias, where the ear capsule shifts backward, the exit of the root of the glossopharyngeus lies behind encephalomere VII, whereas in such forms as the chick and swine, where the ear capsule does not similarly shift backward, the exit of its root is from the expansion of encephalomere VII. In all Vertebrates, the roots of the glossopharyngeus and the Urvagus lie close to each other, but in S. acanthias, where there is a greater amount of posterior displacement than in any other Vertebrate that I have studied, these roots are more crowded together than in other forms. These facts seem to me to warrant the conclusion that the roots of the glossopharyngeus and the Urvagus primitively made their exit from those encephalomeres which give rise to their ganglionic Anlagen. And we may likewise assume that the local thickenings of these encephalomeres have their significance in this primitive relation, i. e. they contained the "Kerne" of these roots. I am able to find no facts which render this assumption untenable.

---

[1] Part of the neural-crest cells surrounds the mesoderm of the visceral arches, and very probably gives rise to some of the connective tissue of the arches. (See Plate **6**, Fig. 40, *cl. crs. n.*) Whether or not they later form the cartilages of the arches, as they are said to do in Necturus (Platt, '94, '97), is a question which requires more careful and prolonged study than I have been able to give.

On the other hand, encephalomere IV never has nervous connection with a visceral arch. From it few neural-crest cells are proliferated, and in consequence it never forms the ganglionic Anlage of a nerve, nor does it ever in ontogeny have a motor nerve in connection with it. Since the other four encephalomeres are related to visceral arches, I incline to think that this encephalomere was once related to a visceral arch of its own. Otherwise, so far as I can see, its existence is inexplicable. In this condition, then, I find additional evidence of a lost visceral arch, which van Wijhe ('82), Miss Platt ('91^a), and Hoffmann ('94) believe once existed in the region of this neuromere. These investigators have found a want of exact correspondence between the somites and the visceral arches in the region of the spiracular cleft. Van Wijhe was led to believe that the *hyoid* (2d visceral) arch is double, — i. e. represents two arches, the fusion of which has resulted in the obliteration of the visceral cleft between them, — while Miss Platt and Hoffmann have held that the *mandibular* arch is double, and that an anterior gill cleft has disappeared. The disappearance of a visceral cleft is rendered plausible, if we assume that such a loss would greatly strengthen the mandibular arch when it came to function as a lower jaw. The evidence from a study of mesomerism and neuromerism therefore seems mutually confirmatory.

If encephalomere IV was related to a lost visceral arch, it follows that the lost arch must have been situated posterior to the mandibular (1st visceral) arch, for the musculature of this arch is innervated from encephalomere III. It also follows, because of the relation of the nerve of encephalomere V (facialis) to the present spiracular cleft, that this was once the second visceral cleft instead of the first (disregarding for the present the possibility that the mouth represents a pair of gill clefts), as it now is. It seems entirely possible that the outpocketing of the present first visceral (hyo-mandibular) cleft was originally a double one,[1] and that the fusion of these two outpocketings resulted in the loss of the visceral arch which once separated them, and therefore in the loss of the nerve primitively related to that arch. Moreover, between the second head somite of van Wijhe, which extends into the mandibular arch, and the fourth somite, which is widely connected with the mesoderm of the hyoid arch, there lies the third head somite, in correlation with which there is no intermediate visceral arch. This somite (the 3d) lies opposite the posterior constriction of neuromere IV, and speaks plainly for the previous existence of a lost head segment, for which neuromere IV may once have furnished the nerve centre. Did such an arch exist, each of van Wijhe's somites from the second to the sixth, and each of the encephalomeres from III to VII would correspond with a visceral arch.

I give a brief summary of the line of reasoning which leads me to believe that the significance of the hindbrain neuromeres lies in their primitive relationship to the visceral arches. In the young embryos of S. acanthias two facts, both so far as I know new, present themselves. In the first place, the hindbrain neuromeres, five in number, are found to be successive similar thickenings of the lateral zones of the medulla. Secondly, from four of them, viz. III, V, VI, and VII, are proliferated the ganglionic cells of the four cranial nerves which innervate the first four visceral arches, viz. the trigeminus, the facialis, the glossopharyngeus, and the Urvagus. A clue to the significance of the local thickenings of the neural wall in the tract of the encephalomeres is given in the fact that from those two encephalomeres which (in other Vertebrates as well as in S. acanthias) most closely retain these primitive nerve relationships, viz. III and V, emerge the fibres which innervate the visceral arches (primitively) related to them. The thickenings are the first expression of the "Kerne" (nuclei) of the nervous centres related to the visceral arches, and possibly also, primitively, of those related to the somites.

---

[1] Kupffer ('93) finds in Acipenser embryos an entodermal outpocketing or pouch, which soon disappears, just anterior to the hyomandibular pouch. The position of this pouch would identify it with the cleft whose former existence seems probable on the evidence given above. Houssay ('91) also recognizes in Amblystoma a visceral cleft between the oral and the hyomandibular.

A study of neural segments anterior and posterior to the medulla has led me to the conclusion that the *local thickening* is a more essential characteristic of a hindbrain neuromere than the commonly accepted criteria, viz. the radial arrangement of cells in the neuromere, and the crowding of them in the regions of constriction between neuromeres, both of which may be the result of mechanical influences.

The shifting of the point of exit of the roots primitively related to encephalomeres VI and VII may easily be explained as the result of the crowding caused by the ear capsule. Since four hindbrain neuromeres are clearly related to four visceral arches, we should expect the remaining one, encephalomere IV, to have been primitively related to a visceral arch. That such an arch has been present in the region of this neuromere during phylogeny, has been made probable by the studies of van Wijhe ('82), Miss Platt ('91), and Hoffmann ('94). The evidences from the study of neuromerism and mesomerism are mutually confirmatory, and to the effect that *a visceral arch has been lost in the region of encephalomere IV and van Wijhe's third somite.* Having established an exact numerical correspondence between encephalomeres and somites (head cavities), and a probable primitive correspondence of hindbrain encephalomeres with visceral arches, I conclude that *in the head region there existed primitively a correspondence between neuromerism, mesomrism, and branchiomerism.* Since this correspondence is not to-day exact in Squalus or in any other known Vertebrate, it seems necessary to discuss somewhat in detail the constituent parts of the anterior or more highly modified metameres, and to inquire what may be inferred as to their previous conditions. The table on the opposite page, although in part theoretical, will help to make the discussion clearer.

I have in this table included neuromeres as far posteriorly as the eleventh. Accepting Hoffmann's ('94) conclusion that vertebral arches as far back as that which corresponds with van Wijhe's tenth somite fuse into the cranium of the adult Squalus,[1] it would follow that neuromeres I to XI would be included in the cranium. The variability in the number of segments added to the occipital region of the cranium in different Selachii and Ichthyopsida (Fürbringer, Sewertzoff) makes the exact number in Squalus a matter of no great morphological importance.

We see that the cephalic segments are highly modified segments altered by reduction or enlargement (possibly even by substitution and change of relation, as, for example, in the case of the vagus segments) of

---

[1] Recently confirmed by Sewertzoff ('98).

Table III.—NEUROMERES I TO XI IN SQUALUS, AND THEIR RELATIONS TO NERVES, SOMITES, AND VISCERAL ARCHES.

	NEUROMERES	I		II		III		IV		V		VI		VII		VIII		IX		X		XI
CEPHALIC METAMERES.	Somites . . .		a[1]		1		2		3		4		5		6		7		8		9	
	Nerves (dorsal)	I (olf.)		ophth. prof. V		V		(V)[7]		VII		IX		X		X		1st sp.[2]		2d sp.[3]		3d sp.[3]
	Nerves (ventral)		lost		III		IV		(VI)		(VI)		(VI)		VI		1st sp.[4]		1st sp.[4]		1st sp.[4]	
	Visceral clefts			lost		mouth		lost		1		2		3		4		5		6		lost[5]
	Visceral arches		?[6]		?[6]		1		(1)		2		3		4		5		6		lost[5]	

[1] Possibly also representing a visceral pouch.
[2] Fuses with the dorsal ganglion of X in later stages.
[3] Represented by ganglia which probably disappear in development.
[4] Form the first three roots of the embryonic hypoglossus nerve.
[5] Found in Hexanchus, Heptanchus, and Chlamydoselachus.
[6] Possibly represented in the two labial cartilages.
[7] Roman numerals bracketed indicate the theoretical nerve relationships.

parts of the original segments. Fortunately, however, with the knowledge that neuromeres and mesomeres correspond numerically, we are able to see that the majority of changes which have occurred are correlated ones, and therefore capable of explanation. We furthermore see that the greatest changes have taken place in the more anterior metameres, chiefly and primarily by the loss of the ventral parts of these metameres. Since the more posterior of the cephalic segments have indubitable metameric value, I shall discuss in detail only those anterior ones (viz. I to VII) concerning which there is most disagreement among morphologists, beginning with the consideration of the seventh, whose relations are least modified.

VIII. Primitive Relations of Cephalic Segments.

a. RELATIONS OF ENCEPHALOMERE VII.

Opposite the posterior constriction of this encephalomere in very early stages lies van Wijhe's 6th somite, which develops embryonic muscle fibres and is universally considered a true somite. I therefore regard this as the mesomere corresponding with encephalomere VII, whose neural-crest cells first meet the mesoderm opposite the anterior constriction of this somite (Plate **3**, Fig. 13). These cells form the Anlage of the anterior branch of the vagus (Urvagus), and I assume that the primitive relations of this nerve were with the myoseptum between the 5th and 6th somites. The intermediate position of the Urvagus with respect to the myotomes and its ontogenetic union with spinal ganglia in some Vertebrates serves to show that there is no fundamental difference in this respect between cranial and spinal nerves. For reasons which will be stated in connection with the study of the relations of encephalomere IV, I regard the abducens (Plate **4**, Fig. 21), whose fibres have their exit from the ventral horn of encephalomere VII, as representing in part the ventral nerve of this segment. Furthermore, I assume that the mesoderm of the 6th somite was primitively connected with the mesoderm of the 4th visceral arch (Plate **3**, Fig. 16); because that somite in Ammocœtes which I regard as its exact homologue, viz. the 2d post-otic somite, is certainly in early stages thus connected. Consequently the present 3d visceral cleft bounds ventrally the visceral (splanchnic) portion of this segment.

b. Relations of Encephalomere VI.

The present structure and relations of the component parts of what I regard as the primitive sixth cephalic segment have been considerably changed cœnogenetically by the development of the otic capsule. Arising from what in all probability was primitively a sensor organ of the dorsal lateral line (Ayers), the great enlargement and subsequent invagination of this capsule bring about ontogenetically the degeneration of the musculature of the 5th somite, whose cells, after assuming the elongated spindle form of embryonic muscle cells, are transformed in early stages into loose mesenchyma. In Ammocœtes, however, only the median portion of the 1st post-otic somite disappears during ontogeny, while the lateral portion forms the most anterior segment of the lateral body musculature (musc. lateralis capitis anterior, von Kupffer). Furthermore, in Squalus the development of the otic capsule causes a shifting backward of the point of exit of the fibres of the glossopharyngeus, whose ganglion cells were proliferated from encephalomere VI; moreover, the fibres of this nerve may be traced in the neural tube as far forward as encephalomere VI, in which, it is my opinion, their nuclei lie. The growing ganglionic Anlage of this nerve meets the mesoderm between the 4th and 5th somites (Fig. 13), and I assume that it was primitively related, as are the dorsal nerves of Amphioxus, to a myoseptum, i. e. the one primitively between somites 4 and 5. The sensor fibres of this nerve innervate the skin of the present 2d visceral cleft (Fig. 14), which was, I assume, primitively inter-somitic in position and situated ventral to the myoseptum between the 4th and 5th somites. Its motor fibres innervate the splanchnic musculature of the present 3d visceral arch, probably a primitive relation. The abducens nerve, I believe, represents the primitive ventral nerve of this metamere.

c. Relations of Encephalomere V.

The fourth somite, the one corresponding to the fifth cephalic segment, is the most rudimentary of all the cephalic somites. The phylogenetic loss of its musculature and the ontogenetic dissolution of its cells into a loose mesenchyma may be explained as due to the same cause as that operative in the case of the 5th somite, the development of the otic capsule. The dorsal nerve of this segment, the facialis, is inter-somitic in position, occupying the constriction dividing the 3d and 4th somites (Figs. 11–17), and its motor fibres innervate the (splanchnic) musculature of the corresponding (2d visceral or hyoid) arch. Correlated with the loss of the somatic musculature of this segment, a somatic (ventral) nerve is wanting, and as in the case of the 6th segment I assume that this is to-day represented by the abducens. Since the sensor fibres of the facialis innervate the skin of the hyomandibular (1st visceral) cleft, this cleft may be believed to have been primitively situated ventral to the constriction between the 3d and 4th somites. I find no evidence to support the view that the hyoid arch represents two splanchnic segments.

d. Relations of Encephalomere IV.

As has already been stated, there is no ganglionic nerve Anlage proliferated from encephalomere IV, and although the fibres of the major root of the trigeminus have their exit in early stages from its outer convexity, the probability is that such relation of nerve V is secondary, and therefore not of phylogenetic significance. I hold that this encephalomere, by virtue of its local thickening, affords evidence of a lost visceral arch, the loss of which would naturally be correlated with the loss of the dorsal nerve. Since, however, the disappearance of the splanchnic portion of this segment may have been due simply to a union with the corresponding portion of the anterior (mandibular) segment, it is also possible that the dorsal nerve has fused with the nerve of the anterior segment, the trigeminus. This conclusion seems indeed supported by the evidence that at least some of the fibres of the trigeminus roots have their nucleus in the lateral horn of this (4th) encephalomere.

In a scheme of primitive segmental relations such as I am at present advocating, there is likewise difficulty in explaining the fact that the somite (van Wijhe's 3d) which I assume to correspond with encephalomere IV is innervated by the abducens, whose fibres make their exit from encephalomere VII. The evidence which leads me to conclude that the abducens to-day represents the primitive ventral nerve of this encephalomere, as well as those of encephalomeres V, VI, and VII, has been partly given in connection with the study of its development; it may be summarized as follows. (1) Its roots are many (4–6 in various Selachii) and more widely separated than those of any other nerve. (2) Not only do abducens fibres innervate pre-otic musculature (musc. rectus posterior), but fibres from this nerve may also be traced for a considerable distance in the mesoderm of the embryo posterior to encephalomere VII (Fig. 20). (3) The variability as to the place where its fibres emerge, as shown by comparative embryological evidence, appears to indicate that its relations are not limited to any single encephalomere. (4) Its nucleus in the ventral horn of the neural tube is greatly elongated.

(5) In Torpedo it innervates musculature (musc. rectus posterior) derived from *two* somites, viz. van Wijhe's third and *fourth* (Sewertzoff, '98). I am not able, however, to offer direct evidence that the nerve has part of its nucleus in encephalomere IV. I am therefore not able to exclude the possibility that the ventral root of a post-otic somite has been substituted for the pre-otic ventral nerve which once innervated somite 3. That such a substitution of the fibres of a ventral nerve of one segment for those of another may take place ontogenetically, I have the following evidence. I find that in a Squalus embryo of 50 mm. the ventral nerve of van Wijhe's 7th somite has become very rudimentary, while fibres from the ventral nerve of the 8th somite extend to the musculature derived from the 7th somite, which in this stage forms the most anterior segment of the lateral musculature. Now, if the ventral root of the 7th somite atrophies before the adult stage is reached, and if the musculature derived from this somite remains the first segment of the lateral trunk musculature of the adult, as has been stated by van Wijhe ('82) and Hoffmann ('94), the conclusion seems unavoidable that we have to do here with a substitution of a posterior nerve for one farther anterior. Moreover, in Petromyzon we have evidence that the first five post-otic myotomes of the lateral trunk musculature are innervated by the ventral nerves of the last two of the corresponding somites, i. e. the 4th and 5th post-otic, which in my opinion are homologous with the 4th and 5th post-otic somites of Squalus (van Wijhe's 8th and 9th). Here also the conclusion seems to me to be warranted that there has been a phylogenetic, if not an ontogenetic, substitution of the nerves of posterior segments for those of more anterior segments.[1] We may therefore infer, with a considerable degree of probability, that a similar substitution of a post-otic nerve for a pre-otic one may have occurred phylogenetically in the case of the abducens. Such evidence, however, seems to render unwarrantable the assumption of a primary and inseparable connection of motor nerve and muscle. Furthermore, the evidence that the motor nerves develop as axis-cylinder processes of medullary cells given by His ('89) for spinal nerves, and by myself in this

---

[1] See Neal ('97, Figure 2, p. 446) for evidence that the fibres of a post-otic ventral nerve (hypoglossus auctorum) extend into the pre-otic region with the muscle they innervate. It would seem a very easy matter for such fibres to come into nervous connection phylogenetically with the eye muscles, and especially the posterior of these, with which in Petromyzon they are very closely connected. Hatschek ('92) stated that the musc. rectus posterior becomes connected with the anterior of the post-otic myotomes. See evidence given by M. Fürbringer ('97) and Neal ('97) upon this question.

paper for cranial ventral nerves in Selachii, leads to the same conclusion. The visceral cleft which defined anteriorly the splanchnic part of the fourth segment is not ontogenetically evident in Squalus. Kupffer ('93) has possibly seen evidence of a rudimentary cleft between the mouth and the hyomandibular cleft of Acipenser. And possibly this cleft may be represented in the "Pseudobranchialrinne" of Amphioxus.

e. Relations of Encephalomere III.

As in the case of the four posterior hindbrain segments, the study of the development of the nerves connected with encephalomere III (Hinterhirn) gives the clue to the primitive relations of this primary vesicle. The neural-crest cells proliferated from it pass ventrally into the mandibular arch. From a part of these a large ganglion is formed (the Gasserian), through which pass the motor fibres, whose nucleus is, at least in part, in encephalomere III, to innervate the musculature of the first visceral (mandibular) arch. We have thus the splanchnic elements of a cranial segment. In the Table of Nerve Relations (p. 253) the trochlearis has been given as the ventral (somatic) nerve of this segment. The evidence in favor of this view has already been stated, and consists in the facts that it innervates musculature derived from dorsal (somatic) mesoderm, that its fibres develop as processes of neuroblasts in the neural tube, and that its histological relations and structure in the adult show it to be a purely motor nerve with motor nucleus in the ventral horn of encephalomere III. I regard the mouth as representing the fused visceral clefts which bounded anteriorly the splanchnic portion of this segment. We have thus all the essential elements of a head metamere.

f. Relations of Encephalomere II.

From the simple dorsal expansion of encephalomere II are proliferated cells which pass ventrally and fuse with the skin to form the mesocephalic ganglion[1] lateral to the 1st somite (Figs. 17 to 20). Although this ganglion never becomes connected with the midbrain (encephalomere II), since its fibres enter the brain through the r. ophthalmicus profundus V, it must in my opinion be regarded as a segmental ganglion comparable with those of the following cranial nerves; the ophthalmicus profundus must likewise be considered as a dorsal nerve homodynamic with the succeeding cranial nerves. Its want of motor fibres may be explained as resulting from phylogenetic loss, since in

---

[1] This ganglion is homologous with the first trigeminus ganglion of Cyclostomes.

Myxinoids this nerve possesses motor fibres (J. Müller, P. Fürbringer, Price), and its segmental value as a dorsal nerve seems thereby established. The fact that the fibres of the ophth. profundus V enter the brain at a point posterior to encephalomere III, instead of anterior to it, as they should in order to conform to my scheme of segmental relations, appears to me no serious objection. That they enter the brain at a point posterior to that at which the motor fibres innervating the mandibular musculature enter, and in consequence cross these fibres in the mesocephalic ganglion, is to be explained by the tendency, especially of the sensor cranial nerves, to enter the brain as near the otic capsule as possible (see Ahlborn, '84^{a}), and by the more conservative relations of the motor fibres (roots) generally.

In my preliminary paper I placed tentatively the so called "thalamic" nerve as the possible dorsal nerve of encephalomere II. Now, however, I question the correctness of this opinion. We certainly need something more than a strand of neural-crest cells which persist for some time in a region of constriction between encephalomeres, but *which never assume fibrillar relation with the neural tube*, to warrant us in assuming that we have to do with a *nerve.*[1]

The development and relations of van Wijhe's first somite and of the oculomotorius leave no doubt that in them we have the somatic elements of a metamere. Probably no ventral or splanchnic portion of the mesoderm of this segment exists, consequently the r. ophthalmicus profundus possesses no splanchnic fibres.[2] In my opinion it is doubtful if the hypophysis may be regarded as evidence of an ancestral visceral cleft between segments I and II.

However, I hold that the structural comparability of encephalomere II with hindbrain encephalomeres, together with the evidence of its relation with a segmental ganglion, and of its connection with somatic musculature by means of a ventral motor nerve, strongly favors the view that it is serially homologous with hindbrain encephalomeres.

g. Relations of Encelphalomere I.

That which I regard as the first cephalic segment of Craniota consists of an encephalomere (primary forebrain) which has been shown to be

---

[1] Kupffer excels Miss Platt in discovering "rudimentary" nerves, but until we have a better criterion for a nerve than a cellular strand there is no reason why the number of "rudimentary" nerves should not be much larger than it is at present recognized to be.

[2] Possibly the skeletogenous element of the ventral portion of this segment is to be found in the "maxillar Lippenknorpel" of Gegenbaur.

morphologically comparable with the hindbrain encephalomeres. It is in connection with a sensor nerve, the olfactory, which appears comparable with the sensor portion of a dorsal segmental nerve in so far as it is composed of bipolar ganglion cells which send their fibres into the brain and, in my opinion, are in part derived from the neural crest. My observations upon this point, however, are as yet incomplete. The want of motor fibres in the dorsal nerve of this segment is correlated with the want of splanchnic musculature.[1] That structure which I, in agreement with Miss Platt ('91) and Hoffmann ('94 and '96), regard as a rudimentary somite (compare Plate **3**, Figs. 16, 17, *cav. a.*), — since it resembles the following somites and gives evidence of producing rudimentary muscle cells, — represents the somatic portion of this segment. In correlation with the want of fully developed musculature, no ventral somatic nerve is present. Van Wijhe ('86^a, p. 680) wrote : "Wenn der Olfactorius ein segmentaler Nerv wäre, müsste man bei demselben das ursprüngliche Vorhandensein eines Somiten und einer zugehörigen ventralen Nervenwurzel annehmen. Von beiden ist keine Spur vorhanden." So far as the somite is concerned, it appears that in the "anterior somite"[2] we now have the requisite evidence. The lateness of the differentiation of the "premaxillar Lippenknorpel" makes it seem at most only remotely possible that it may be regarded as the ventral skeletogenous element of this segment.

h. Comparison with the Segmentation of Amphioxus.

A comparison of the segmentation of Squalus as shown in Table III. (p. 253) with that of Amphioxus is of interest, inasmuch as it appears to favor important conclusions reached by the study of Squalus alone. However, before stating my own conclusions concerning the primitive metamerism of Amphioxus and the homologies of its segments with those of Squalus, it will be well to review the conclusions of previous investigators.

A comparison of their results may be made in the form of a table on the opposite page (after M. Fürbringer, '97, p. 643, slightly modified).

While Hatschek ('92), Willey ('94), and M. Fürbringer ('97) homologize the mouth of Amphioxus with that of Tunicates and Craniota, but

---

[1] Likewise in Amphioxus the anterior dorsal nerve is generally believed to be purely sensor in function.

[2] Van Wijhe ('82) saw the "anterior somite" in Galeus, but unfortunately possessed only one embryo; he was therefore unable to express an opinion concerning its segmental value, based on a knowledge of its development and differentiation.

TABLE IV.

	FATE OF		HATSCHEK, '92.	VAN WIJHE, '93.	WILLEY, '94.
1	Unpaired mouth.		Single persisting mouth, the homologue of the median unpaired mouth of Tunicates and higher Vertebrates.	Primary mouth (Autostoma) pushed toward the left and modified to form the pre-oral pit (Räderorgan).	Single persisting mouth, the homologue of the mouth of Tunicates and higher Vertebrates.
2	1st visceral pouch (vorderes Entodermsäckchen) of Hatschek.	Right.		Perhaps the homologue of the 1st head cavities (1st somites) of Selachii.	Probable homologue of the right 1st (premandibular) head cavity of Craniota.
		Left.	Pre-oral pit (Räderorgan; Sinnesorgan).	Pre-oral pit; also primary mouth (Autostoma).	Pre-oral pit, probable homologue of the left 1st (premandibular) head cavity of Craniota.
3	2d visceral pouch of Hatschek (1st visceral cleft of van Wijhe and Willey).	Right.	Right pseudo-branchial groove.	Club-shaped gland.	Club-shaped gland.
		Left.	Left pseudo-branchial groove.	Secondary permanent mouth (Tremostoma). (Spiracular cleft of Selachii.)	1st (abortive) primary gill slit.
4	3d visceral pouch of Hatschek (2d visceral cleft of van Wijhe and Willey).	Right.	1st permanent right visceral cleft.	Lost.	2d (1st permanent) secondary or right gill slit.
		Left.	1st permanent left visceral cleft.	Lost.	2d (1st permanent) primary gill slit.
5	4th visceral cleft of Hatschek (3d visceral cleft of van Wijhe and Willey).	Right.	2d permanent right visceral cleft.	1st permanent right visceral cleft.	3d (2d permanent) right gill slit.
		Left.	2d permanent left visceral cleft.	1st permanent left visceral cleft.	3d (2d permanent) primary gill slit.

deny its gill-cleft nature (Dohrn), van Wijhe regards it as a visceral cleft on the left side, antimeric to the club-shaped gland, which with Willey he regards as a modified visceral cleft, exactly homologous with the hyomandibular (spiracular) cleft of Craniota. Van Wijhe ('93, p. 155) finds evidence of a primary unpaired mouth in the external opening of the left anterior entodermic diverticulum known as the preoral pit (Räderorgan). Homologizing the "Gehirnanschwellung" of Amphioxus with the "Gehirnblase" of the larvæ of Ascidians, he considers it impossible to homologize the mouth (tremostoma) of Amphioxus with the median dorsal mouth of Tunicates, since in the former the mouth and its antimere are laid down immediately *posterior* to the brain vesicle, whereas in the latter the mouth arises in the median plane immediately *anterior* to the brain vesicle; however, the *visceral clefts* of the young Ascidian larva are laid down, like the mouth of Amphioxus, immediately behind the brain vesicle. Moreover, van Wijhe holds that the mouth of Amphioxus is an organ of the left side only, and on the following grounds (quoted from Willey, '94, p. 178): "The outer muscle of the oral hood represents the anterior continuation of the *left half only* of the transverse and subatrial muscles. The inner nerve-plexus of the oral hood is formed on both sides exclusively from nerves which arise from the left side of the central nervous system. The velum is innervated entirely from nerves of the left side," viz. branches from the 4th, 5th, and 6th left dorsal nerves.

Willey ('94) finds evidence to support his view, that the mouth of Amphioxus represents the median dorsal mouth of Ascidians, in the marked asymmetrical conditions of the larva, for which van Wijhe's observations and conclusions afford no explanation. Affirming the asymmetry to be non-adaptive and non-advantageous (*contra* Korschelt und Heider), he concludes that it is the mechanical result of the (phylogenetic) forward extension of the notochord, an extension which is advantageous to an animal which bores in the sand. Hatschek ('92) and M. Fürbringer ('97) agree with Willey in this explanation as to the homology of the mouth of Amphioxus, but bring forward no evidence to support their view. There is no disagreement in homologizing the anterior entodermic diverticula (vordere Entodermsäckchen) of Amphioxus with at least part of the premandibular head cavities (1st somite of van Wijhe) in Craniota.

From the foregoing review it will be seen that two very important questions concerning the nature and homologies of the Vertebrate mouth remain in dispute, viz.: — 1. Is or is not the mouth of Amphioxus to be homologized with the mouth of Ascidians? 2. Is it or is it not homologous, either wholly or in part, with the mouth of Craniota? Upon the answer to the former question would seem to depend the settlement of the question whether the mouth of Amphioxus may or may not be regarded as a visceral cleft, for there is no reason to believe that the mouth of Ascidians represents a pair of visceral clefts. Notwithstanding that Willey appears to have in the asymmetrical mouth of Amphioxus strong evidence in favor of his homology, which has also met the approbation of Marshall ('93), I consider the different relation of the Tunicate and Vertebrate mouth to the brain vesicle a very serious objection to his theory. Furthermore, the presence of a preoral intestine in Vertebrates, which in Squalus extends (morphologically) anterior to the infundibulum, — even to the neuropore, as does the intestine of Tunicates, — leads me to agree with Beard, Kupffer ('88 and '91), and van Wijhe ('94), that in the present mouth of Vertebrates we have a *neostoma,* and also that a *palæostoma* homologous with that of Tunicates must be sought in an anterior opening of the preoral intestine. Kupffer finds evidence of this *palæostoma* in the ectodermic invagination of the hypophysis towards the "Preoraldarm," while van Wijhe finds it in Amphioxus, as stated in the Table, in the actual opening of the preoral intestinal diverticulum of the left side as the preoral pit (Räderorgan).

Waiving the question as to which, if either, of these theories is correct, I regard the mouth of Ascidians as opening at the morphologically anterior end of the alimentary canal; for there appears to me nothing in the literature upon Tunicates to show the presence of a preoral intestine in these forms. The mouth of Appendicularia, which has no "preoral lobe," (though homologized by Willey with the preoral intestinal diverticula of Amphioxus and the premandibular cavities of Craniota,) has a terminal position.[1] According to Willey the method of formation of the preoral lobe in those Ascidians possessing such is as follows (p. 218): "When the larva first hatches, the entoderm and ectoderm are in contact with one another at the anterior extremity of the body, just as they are in the earlier stages. Soon, however, the ectoderm, with the adhering papillæ, springs away from the endoderm at this point, leaving a space into which the two lateral mesodermic bands force their way. In this way a special anterior portion of the body cavity, præoral and præenteric, is produced, and is at first completely filled by a compact mass of rounded cells derived from the mesodermic bands. . . . The anterior, or præoral portion of the body cavity, of which we have just traced the origin, is, and subsequently becomes in a still more pronounced way, the *cavity of the snout*, or *præoral lobe*."

---

[1] Willey ('94, p. 277) writes: "Whatever the truth may be as to the precise systematic position and phylogenetic value of Appendicularia, one thing, to my mind, remains absolutely certain, namely, that it has descended from a form which possessed a præoral lobe, and that it has secondarily lost that structure."

On the other hand, the preoral "head cavities" of Amphioxus, which Willey homologizes with the "preoral lobe" of Ascidian larvæ, are formed, as stated by Hatschek ('81), from an abstricted portion of the preoral archenteron. The differences in the formation of these two structures, therefore, seem too striking to permit their being considered completely homologous with each other.

Evidence has already been given in this paper which, in my opinion, makes it impossible to homologize the preoral "head cavities" (anterior entodermic diverticula) of Amphioxus with the "premandibular head cavities" of Craniota. The morphologically anterior portion of the archenteron, the "anterior head cavities" (Platt), are the only structures in higher Vertebrates which, in my opinion, can be homologized with the "head cavities" of Amphioxus. Homologizing, therefore, the "anterior head cavities" in these two forms, I submit on the opposite page for comparison with Squalus the table of the anterior eleven segments in Amphioxus as I interpret them.

If we compare Tables III. (p. 253) and V., we find the following fundamental resemblances in the segments of Squalus and Amphioxus.

Of the component elements of the *first segment*, that which I have regarded as the somatic element, consists of paired cavities cut off from the anterior portion of the archenteron. Since in both cases these cavities represent ventral as well as dorsal and lateral portions of the archenteron, it is impossible to contend that they contain only the mesodermic element of the segment. It seems not improbable that potentially they represent also the visceral-pouch element between this and the following segment. The opening of the left of these in Amphioxus to the exterior as the preoral pit may be regarded as evidence favoring this view. Moreover, M. Fürbringer ('97, p. 633) finds a late differentiated and rudimentary myotome, which lies anterior to the dorsal paired nerves II, which would, if present as stated by him, represent the mesodermic element of this segment, and the "anterior head cavities" would in consequence necessarily be regarded as modified or abortive visceral pouches, as held by Kupffer. Since my sections of Amphioxus give me no evidence of this rudimentary myotome, I hold

TABLE V. — METAMERISM OF AMPHIOXUS.

SEGMENTS	I		II		III		IV		V		VI		VII		VIII		IX		X		XI		XII	
Somites		a[1]		1		2		3		4		5		6		7		8		9		10		11
Dorsal nerves	I		II		III		IV		V		VI		VII		VIII		IX		X		XI		XII	
Ventral nerves		lost		1		2		3		4		5		6		7		8		9		10		11
Visceral clefts (r.)			lost		c.s.g.[2]		lost		1*		2*		3*		4*		5*		6*		7*		8*	
" " (l.)			lost		M.[3]		1		2*		3*		4*		5*		6*		7*		8*		9*	

[1] Possibly representing also a visceral-pouch element.

[2] Club-shaped gland.

[3] M. Mouth.

The permanent visceral clefts are indicated by asterisks.

with van Wijhe, Hatschek, and Willey, that the first myotome in Amphioxus is situated behind the first two pairs of nerves, and also that the "anterior head cavities" of Amphioxus represent the somatic elements of the anterior segment in Craniota. From this point of view, the different fates which the two cavities in Amphioxus undergo, as well as the loss of musculature, is to be regarded as cœnogenetic. The dorsal nerves in both forms are exclusively sensor in correlation with the loss of splanchnic musculature.[1] The unpaired olfactory of Amphioxus is to be compared with the long persisting median connection of the neural tube and olfactory plate in Squalus (*lobus olfactorius impar*, Kupffer). No somatic musculature and no ventral nerves are developed. I regard the cerebral vesicle of Amphioxus, since it is limited posteriorly by the tuberculum posterius (Kupffer), as homologous with the primary fore-brain of Squalus, and therefore as the neuromeric element of the first segment.[2] Whether or not the visceral cleft of this segment is represented in the "anterior entodermic diverticula" (anterior head cavities), I am not able to assert with any degree of positiveness. Fürbringer's discovery appears to favor this view.

In the *second segment* a well developed myotome and ventral nerve develop. In both forms the dorsal nerve of this segment appears to be exclusively sensor. In Myxinoids, however, the dorsal nerve (ophthalmicus profundus) has motor fibres, and it appears to me not improbable that such will be found in its homologue in Amphioxus.[3] If the visceral-cleft element in this segment is not represented in the "anterior head cavities," this may be assumed to have disappeared phylogenetically. All the components of the *third segment* are present, viz. somatic and splanchnic musculature, dorsal and ventral nerves, and visceral clefts.

---

[1] The homology of the olfactorius (I) with the first paired nerve of Amphioxus has already been asserted by Owen (1866). The first paired nerve of Amphioxus according to Owsjannikow (1866) and Rabl ('89) is homologous with trigeminus; with r. orbito nasalis or r. I. trigemini (Huxley, 1874); with opticus (Schneider, '79); with part of trigeminus (Rohon, 1881, and Krause, 1888); with ophth. prof. trig. (Hatschek, '92); and with nervus apicis (van Wijhe, '93).

[2] Kupffer ('93) homologizes the cerebral vesicle of Amphioxus with the Vorhirn (Vorderhirn and Mittelhirn) of Craniota.

[3] The second paired nerve of Amphioxus has previously been homologized with part of trigeminus by J. Müller (1842), W. Müller (1875), and Krause (1888); with trigeminus by Goodsir (1841); with trigeminus and vagus by Quatrefages (1845) and Owen (1866); with facialis by Owsjannikow (1867); with opticus by Hasse (1876); with part of trigeminus and with facialis by Rohon (1881); with acustico-facialis by Rabl ('89); with trigeminus exclusive of ophth. profundus by Hatschek ('92); and with ophth. profundus by van Wijhe ('93).

I regard the mouth of Amphioxus as homologous with the left half of the mouth of Craniota and the club-shaped gland as its antimere. That the mouth of Amphioxus as an organ of the left side is exactly homologous with the left half of the mouth of Squalus appears to me probable on the *a priori* ground that it is improbable that an organ of the same function should be twice acquired in the Vertebrate series; and also because the region of fusion of endoderm and ectoderm to form the mouth cleft is in both these forms ventral to the constrictions which separate the second and third mesodermic segments (1st and 2d myotomes). The club-shaped gland also appears as an entodermic diverticulum below the constriction between the second and third mesodermic segments of the right side, that is, opposite the mouth diverticulum, and I therefore, in agreement with van Wijhe ('93), regard it as the antimeric gill cleft.[1]

In the *fourth segment* the following points of resemblance are to be noted. Somatic musculature and a somatic ventral nerve are present. While in Squalus the pair of visceral clefts which bounded anteriorly the splanchnic portion of this segment have disappeared, leaving no trace behind except in the neuromere with which they were connected, in Amphioxus only the right visceral cleft has been thus lost. The left visceral cleft, however, disappears ontogenetically without leaving a trace behind it. A further difference in the two forms appears in the fact that, whereas in Squalus the dorsal nerve has disappeared (or fused with the trigeminus), the dorsal nerve of the left side in Amphioxus is the first of the nerves which innervate the musculature of the velum (van Wijhe).

With the *fifth segment* in both forms begin the permanent visceral clefts. In agreement with Willey ('94), I regard the first secondary cleft as antimeric to the second primary cleft. Their fusion with the ectoderm below the mesodermic constriction between mesoderm segments 4 and 5 (myotomes 3 and 4) is the evidence for their relation to this, the fifth segment. I therefore consider *the first pair of permanent visceral clefts in Amphioxus as the exact homologues of the hyomandibular clefts of higher Vertebrates.* As has already been stated by Willey ('94), all except eight of the primary clefts (starred in the table), which become paired with eight antimeric clefts, undergo atrophy. In conse-

---

[1] Willey ('94) gives reasons for regarding the club-shaped gland as the antimere of the first primary visceral cleft. His reasons are based on topographic relations in stages when the primitive topographic relations are considerably changed, and they seem to me less strong than the reasons stated by van Wijhe and myself.

quence there is found at the end of the larval period a "critical stage" of considerable duration, when *Amphioxus possesses eight visceral clefts, which*, if the homology above be correct, *are exactly homologous with the eight morphological clefts of Heptanchus* (*Selachian*) *and Petromyzon* (*Cyclostome*). The evidence of the exact homology of the mouth and visceral clefts of Amphioxus at its critical period with those of Craniota appears to me strongly confirmatory of the truth of the exact homology of segments in Amphioxus and Squalus as stated above.

i. GENERAL CONCLUSIONS.

The exact numerical correspondence of neuromeres (encephalomeres) and somites has been found not to be a purely accidental one. The ventral motor nerves (oculomotorius and trochlearis) of two successive encephalomeres, viz. II and III, are connected with two successive somites, viz. van Wijhe's 1st and 2d, and the nerves VII, IX, and X (Urvagus), by their topographic relations to successive somites 4, 5, and 6, show a similar metameric correspondence between encephalomeres and somites. Where correspondence does not clearly exist to-day, as in the case of the abducens nerve, we have developmental evidence which suggests how such modifications may have taken place.

Thirteen years ago Ahlborn ('84^a), as a result of his examination of the evidence presented by van Wijhe ('82), stated it as his conclusion that in the head we have a dysmetameric neuromerism, which no longer repeats the metamerism of the mesomeres (somites), but is related to a series of other conditions dependent on both ectoderm and entoderm. Ahlborn likewise concluded that branchiomerism and mesomerism do not correspond. "Gegenbaur's assumption, that the segmentation of the cranial nerves, related as they are to visceral arches, is comparable to the segmentation of the spinal nerves, which correspond with somites, still remains to be proved." The evidence presented above certainly tends to make the assumed correspondence of mesomerism and branchiomerism more probable, and thus indirectly to prove the homodynamy of the nerves which innervate mesomeres and branchiomeres. The recent evidence presented by Hatschek ('92), Kupffer ('91, '96), Price ('96), and Miss Platt ('97) from their studies on Amphioxus, Cyclostomes, and Amphibia points in the same direction, and thus favors Gegenbaur's assumption. The comparative embryological evidence which has been given shows, however, that the adoption of Gegenbaur's view by no means necessitates the assumptions later made by him ('87), viz.: (1) that the head primitively ended with van Wijhe's 6th somite;[1] (2) that between this and the following somite segments (dorsal as well as ventral) have been phylogenetically lost; and (3) that the head primitively ended with the gill region. It has been shown, I believe, that the probable phylogenetic and actual ontogenetic disappearance of visceral clefts does not necessitate the loss of the corresponding mesomere and neuromere. It is true that we have very good reason to infer a phylogenetic loss of distinctly differentiated somites and neuromeres in the Vertebrate series. It is also true that we find evidence of an ontogenetic disappearance of mesomeres. Nevertheless such evidence does not prove that somites have been phylogenetically lost from the occipital region before the group of Selachii, of which Squalus is one of the most primitive forms, is reached. I believe that the evidence which has been given of the complete metameric correspondence of neuromeres and mesomeres — that the Selachian embryo is in this respect an unbroken continuum — renders it unnecessary to assume that somites have been so completely lost that no traces of them appear phylogenetically in Selachii. It is no longer necessary to assume a palingenetic portion of the Vertebrate head which ended with the sixth visceral arch of Selachii (Gegenbaur), or an exact homology between the hypoglossus roots (surely a most uncertain "fixed point") of adult Vertebrates (M. Fürbringer). The evidence which I have given seems thus to favor the opinion of Sewertzoff ('95), that we have "keinen Grund, vorauszusetzen, dass zwischen den palingenetischen Somiten v. Wijhe's (I–VI) und den coenogenetischen (VII–IX) ein Wegfallen der Segmente stattgefunden hat. Wir sehen sine vollkommen regelmässige Anlage der Kopfsomiten und ein eben so regelmässiges [ontogenetic] Verschwinden derselben."

I am aware, however, that the structural differences between the hindbrain neuromeres, e. g. IV to VII, and the neuromeres immediately

---

[1] The suggestion that the gill region is not confined to the head region was first made by Huxley ('58). I believe that direct evidence in favor of this suggestion is furnished by Amphioxus (Hatschek, '92), and by Myxinoids (Price, '96). In this connection, moreover, it is of interest that in my previously ('97) made homology the *last* visceral cleft in Ammocœtes primitively bounds *posteriorly* the segment which is homologous with the *last* cranial segment (Hoffmann, '94) of Squalus, viz. van Wijhe's 10th somite. Furthermore it has been shown (p. 268) that this last visceral cleft of Petromyzon is exactly homologous with the last visceral cleft of Amphioxus in its "critical stage" of development. It should, however, be noted that there have been published three other interpretations of homologies between Selachii and Cyclostomata, differing from that made by me, viz. those by Ahlborn ('84^a), by Hatschek ('92), and by Sewertzoff ('95).

following these may seem to favor Gegenbaur's view that the former belong to a palingenetic portion of the Vertebrate head which ended with the 6th (van Wijhe's) somite (bounding neuromere VII posteriorly and ventrally). The structural gap between the seventh and eighth neuromeres is not, however, so sharp that it should outweigh evidences of similarity, and especially the evidence that somites 6 and 7 are indisputably serially homologous. I must confess that I cannot see that the assumption of palingenetic and cœnogenetic portions of the Vertebrate head has added to the clearness of our morphological conceptions, nor can I see that it is rendered necessary by any ontogenetic or phylogenetic evidence now in our possession. Note, furthermore, the disagreement of opinion as regards what is and what is not *palingenetic* or cœnogenetic among those who have been prominent as advocates of this view, viz. Gegenbaur ('87), his pupil, Fürbringer ('97), and Miss Platt ('97). While Gegenbaur holds that van Wijhe's 6th somite is palingenetic, Fürbringer regards the 6th, and possibly the 5th and 4th somites, as *cœnogenetic*. Miss Platt, on the other hand, believes that the 4th and 5th somites are palingenetic, but that the 6th somite is probably cœnogenetic. All this appears to me confusing and unnecessary. The terms cœnogenetic and palingenetic are purely relative terms. I hold the view that each metamere of the head may be regarded as cœnogenetic in comparison with the metameres anterior to it, the head gradually receiving accessions from the trunk. Gegenbaur's famous "Kritik" of 1887 appears more an attempt to establish the visceral arches as the *essential* criteria of cephalic metameres, than a wholly unprejudiced effort to weigh the evidence both anatomical and embryological which was at his command. I believe that the evidence given in the present paper tends to strengthen the generally accepted opinion, which Gegenbaur has sought to overthrow, that the mesomeres in the head, like those in the trunk, afford the most trustworthy criteria of metamerism. The dorsal (neuromeric and mesomeric) segmentation must be regarded as more conservative than the ventral (branchiomeric or splanchnic) segmentation. The lost elements are chiefly the ventral ones. Their loss has indirectly caused the losses in the dorsal elements, such as the disappearance of splanchnic motor fibres from dorsal nerves and (?) of the thickening of the lateral zones of encephalomeres I and II.

It appears to me that the evidence now in our possession gives reason to hope for an eventual solution of the head problem, not only as regards the nature, but also the number of head segments. The problem, it is true, is easier for occipital than for pre-occipital segments. The serial homology of occipital with trunk segments is not generally questioned at present. A comparison of the integral parts of occipital and trunk metameres shows that the belief in their serial homology is well founded. It must, however, be admitted that occipital metameres show no evidence of either excretory or reproductive organs. Nevertheless we may readily believe from the evidence of these organs in the gill region of Amphioxus that this is a cœnogenetic loss in the Vertebrate series. The chief grounds for belief in the homology of trunk and occipital metameres are these: (1) Occipital somites with their (2) ventral nerves are undoubtedly the serial homologues of trunk somites with their ventral nerves. This evidence alone has convinced most morphologists. But there are still other reasons. With our present knowledge, we may, I think, affirm that (3) dorsal occipital (or cranial) and dorsal spinal nerves are serial homologues. One by one, since the discovery by Schneider ('79) of ventral nerves in Amphioxus, the differences between dorsal spinal and cranial nerves, which were at one time or another maintained, have been with increased comparative embryological and anatomical knowledge shown to be unessential. The evidence given by Schneider ('79), Hatschek ('92), and van Wijhe ('93) shows that dorsal nerves, as seen in Amphioxus, are mixed in function, innervating the skin and splanchnic musculature, while ventral nerves are motor in function, innervating somatic musculature. The typical cranial nerves of Craniota, viz. V, VII, IX, and X, are morphologically comparable with the dorsal nerves of Amphioxus, and are therefore to be regarded, as Balfour for other reasons regarded them, more primitive than the *spinal* nerves, which lack the lateral and dorsal (except in Cyclostomes) cutaneous branches.[1] The recent researches of von Lenhossék ('90), Ramon y Cajal, and Kölliker, by demonstrating the existence of non-ganglionic fibres in the dorsal spinal nerves of Craniota, which by their relations must be regarded as motor in function, have shown that in this respect spinal nerves do not differ from cranial. Moreover, in view of the evidence given by Goronowitsch ('92), Sewertzoff ('95), Neal ('97), and Miss Platt ('97), it can no longer be

---

[1] The place of these branches has been usurped by the lateral branches of the vagus, as I believe has been suggested by Eisig. The advantage in greater centralization is obvious. If it be true, and it is generally admitted, that cranial nerves receive cells from the skin while the spinal nerves do not, an explanation of this also is seen in the extension of the vagus and the concomitant loss to spinal nerves.

truthfully said that cranial nerves differ from spinal in that the former extend laterad and the latter mediad of the mesomeres. We must conclude that dorsal nerves were in all probability, as in Amphioxus, related to the septa between myotomes. Finally, the distinction made by His, in the case of dorsal cranial nerves, between dorsal (sensor) and lateral (motor) *roots*, has, with the knowledge of the facts above stated, an anatomical and physiological rather than a morphological interest. I therefore see no escape from the conclusion that the occipital region of the head is not a region *sui generis*, and I pass to the consideration of the pre-occipital segments.

To those who are deeply impressed with the differences between post-otic and pre-otic regions of the Vertebrate head, it is necessary to emphasize the following fundamental resemblances in the segments of these two regions. (1) Pre-otic and post-otic encephalomeres have been shown to be morphologically comparable. (2) The dorsal nerves connected with these, and (3) the visceral arches which these nerves supply are in these two regions serially homologous. Moreover, as evidence pointing in the same direction, it may be stated that (4) a post-otic nerve innervates pre-otic musculature. Furthermore, the serial homology of pre-otic and post-otic somites appears established by the fact that (5) a pre-otic somite (van Wijhe's 3d somite) is a segment of the dorsal mesoderm. That it is such seems clear, for it is defined anteriorly and posteriorly by well marked constrictions (observed by several investigators), it becomes differentiated into myotome and sclerotome, and its musculature appears first in its median wall, and becomes innervated by a ventral nerve (abducens) serially homologous with ventral spinal nerves. The fact that the primitively dorsal mesoderm of the pre-otic region grows ventrally to form the splanchnic musculature, as has been stated for Cyclostomes, Selachii, and Amphibia, is not a basis for a fundamental distinction between post-otic and pre-otic regions, since this is the method of formation of splanchnic mesoderm throughout the length of the body in Amphioxus. In this respect, as in respect to the nerves, the head shows more primitive conditions than the trunk. Since the literature of the last decade and a half shows little agreement of opinion as to the morphology of the eye-muscle nerves, more especially the oculomotorius and the trochlearis, and since in the preceding pages evidence has been given which tends to reconcile existing differences, it is important to consider briefly the bearing of their morphology upon that of the pre-otic segments. The more recent attempts to classify the eye-muscle nerves as dorsal, lateral, or ventral indicates that the point of view of morphologists is now fundamentally different from that of the older anatomists, who, in dealing with the question of the segmental value of cranial nerves, excluded the eye-muscle nerves from consideration on the ground of their inconstancy in appearance and distribution. Except on the part of Froriep, Kastschenko, and Rabl, who regard the pre-otic region as one *sui generis,* I find no tendency to revert to the view of Stannius ('49, p. 125) that "der Parallelisirung der Augenmuskelnerven mit Spinalnerven stellen sich, wegen ihrer eigenthümlichen Ursprungsverhältnisse, des ihnen zukommenden Mangels von Ganglien und der ausschliesslichen Vertheilung ihrer ungemischten Primitivröhren in den, auch ihrerseits mit Muskeln der Wirbelsäule durchaus nicht vergleichbaren, Muskeln eines Sinnes-Apparates so unüberwindliche Schwierigkeiten entgegen, dass von einer solchen nicht füglich die Rede sein kann." However, the labors of comparative anatomists, among whom may be named Huxley, Gegenbaur, M. Fürbringer, and Schwalbe, during the thirty years following the work of Stannius just quoted, resulted in so well establishing the "Bürgerrecht" of the eye-muscle nerves that morphologists now assume that they are comparable with either dorsal or else ventral segmental nerves. Only a minority of anatomists, among whom may be named Schneider ('79), van Wijhe ('82), Beard ('85), His ('88^a), Dohrn ('91), Neal ('96), and M. Fürbringer ('97), have regarded them as ventral segmental nerves. The weightiest well established evidence in favor of this view was first stated by His ('88), and consists in the fact that the eye-muscle nerves, at least of the adult, resemble ventral spinal nerves both in histological structure and in the situation of their motor nucleus in the ventral horn of the neural tube; and also in the less well established fact that they innervate musculature derived from segments of the dorsal mesoderm. On the other hand, the majority of morphologists, among whom may be named Balfour ('78), Marshall ('81), Dohrn ('85, '87, '90), Gaskell ('89), Hoffmann ('89, '94), Oppel ('90), Houssay ('90), Platt ('91), Froriep ('91), Zimmermann ('91), Hatschek ('92), Mitrophanow ('92, '93), and Kupffer ('94, '95, '96), while in general of the opinion that the abducens is the homologue of one or more segmental ventral nerves, have held that either the trochlearis or the oculomotorius, or both, represent dorsal (or lateral) segmental nerves. The chief arguments in favor of this view consist in evidence (1) of the development of these nerves from neural-crest cells; (2) of a cellular or so called ganglionic structure of the nerves in the embryo; (3) of transitory or permanent ganglia in connection with them; and (4) of the development of at least a part of the musculature innervated by them from splanchnic mesoderm. Thus there is to-day a distinct conflict as to the morphology of the eye-muscle nerves, one party to the conflict being supported by histological evidence, the other by embryological. The assumption by His ('88), that the eye-muscle nerves develop as processes of medullary cells (neuroblasts), — which is involved in his contention that they are the serial homologues of ventral spinal nerves, — has never hitherto received the requisite embryological confirmation. In fact, the latest embryological evidence concerning the development of the oculomotorius and trochlearis seems quite irreconcilable with the view of Schneider ('79), van Wijhe, and His. In regard to the latter nerve, Hoffmann ('89, p. 338) says, if one disregards the fact that no ectodermal fusion takes place, "so gleicht die Anlage des Trochlearis in sehr jungen Entwicklungsstadien [of Lacerta] vollkommen der eines segmentalen Kopfnerven, besonders der des Trigeminus." Froriep also finds that the trochlearis possesses in early stages a ganglion, and is differentiated from neural-crest cells *in situ.* Miss Platt ('91^a, p. 259) likewise states that "in Acanthias the development of the trochlearis in all essential respects so completely corresponds to that of the trigeminus and facialis, that like them it must be considered to combine primarily those dorsal and ventral elements which have separate roots in the nerves of the trunk. It can, therefore, not be regarded as the ventral root of another segmental nerve." Moreover, Kupffer ('95, '96) finds the trochlearis to possess in Ammocœtes both dorsal and ventral roots.

With regard to the oculomotorius, the conclusions of embryologists are even more conflicting. While Dohrn ('91) finds that this nerve is formed by the migration of cells from the ventral wall of the midbrain, and considers it a motor nerve, Miss Platt ('91^a) states that she has shown the oculomotorius to be "undoubtedly originally sensory." Her observation that the nerve develops from the ganglion toward the brain has been confirmed by both Mitrophanow ('93) and Sedgwick ('95). Nevertheless the evidence which has been stated by me in division VI. shows conclusively, as I believe, that all the eye-muscle nerves, oculomotorius, trochlearis, and abducens, develop, like ventral spinal nerves, as processes from neuroblasts lying in the ventral horn of the medullary tube. Therefore, from their development, as well as their adult histological structure and relationships, the eye-muscle nerves must be regarded as the serial homologues of ventral spinal nerves. Finally, with the accumulating evidence given by many investigators, — among them Beard, Dohrn, Ayers, and Kupffer, — that the complicated sensory organs of ear, eye, and nose are differentiations of lateral-line sense organs, we may conclude that there exist no fundamental differences in *nature* between pre-otic and post-otic segments.

The *number* of cephalic segments in the post-otic region (Sewertzoff, Fürbringer) appears to be variable in different Vertebrates. If the estimate given by Hoffmann ('94) for Squalus be correct, there are six post-otic cephalic segments in that form. In the otic and pre-otic regions, I hold the number to be not greater than six,[1] and the exact numerical correspondence of neuromeres and somites very strongly supports the estimate of six, which accords very closely with that made, upon similar but not identical grounds, by van Wijhe, Beard, Marshall, and Miss Platt. I cannot agree with Hoffmann ('96) and M. Fürbringer ('97), who — from the evidence that there is one more mesodermal segment (viz. the "anterior") in Squalus and Galeus than in other known Selachian embryos — conclude that still other anterior mesodermal segments have phylogenetically disappeared, and that it is therefore impossible for us to estimate the number of pre-otic segments. *We have quite as little reason to believe that somites anterior to Platt's have disappeared, as we have to believe that encephalomeres anterior to encephalomere I (the primary forebrain) have once existed.* In the exact numerical correspondence of neuromeres and somites we have, not only evidence of the serial homology of head and trunk segments, but the means to determine their number in the pre-otic region.

IX. Summary.

I am unable to regard Locy's "neural segments" as segments in the true sense of the word, because I find them irregular in size, inconstant in number, bilaterally asymmetrical, and without definite relation to structures known to be segmental. They are phenomena connected with the proliferation and disassociation of the cells of the neural crest.

The posterior boundary of the cephalic plate coincides with the posterior boundary of encephalomere VI, opposite which the auditory invagination takes place.

Orr's criteria for hindbrain neuromeres hold good only for the later stages of development of S. acanthias. In the early stages of this animal, the neuromeres are local thickenings of the lateral zones, as well as dilatations of all of the zones of the medulla. As paired glangionic enlargements of the central nervous system, they obviously resemble, except in position, the ventral chain of ganglia of Annelids. Therefore they cannot be explained as the passive result of mechanical shoving or bending. The constrictions between the neuromeres, as well as the crowding of nuclei in the regions of constriction, may however be, and most probably are, intensified by shoving or bending of the neural tube.

---

[1] Six neuromeres alternating with five somites. With Miss Platt ('94) I hold that the otic sense organ was primitively situated above the constriction between van Wijhe's 4th and 5th somites.

No structural conditions are presented by the myelomeres which are not reconcilable with the hypothesis that their existence is dependent upon the presence of the mesodermal somites. If they ever possessed a dorsal segmentation like that of the "hindbrain neuromeres," — and there is no evidence to show that they ever did, — it has been lost. But, though they appear of doubtful morphological value, their numerical correspondence with nerves and somites attests their metameric value.

The so called neuromeres of the forebrain and midbrain (encephalomeres of Zimmermann) are not morphologically comparable with "hindbrain neuromeres," since they are simply dorsal or ventral expansions which are secondary in the time of their appearance. I hold that there are much better reasons — viz. on the grounds of time of appearance, of structure, and of relation to nerves and somites — for regarding each of the primary forebrain and midbrain vesicles (neuromeres I and II) as serially homologous with hindbrain neuromeres (neuromeres III to VII), than for so regarding their later subdivisions. The latter are cœnogenetic vesiculations of the neural tube, and not of metameric value.

Both dorsal ganglia and ventral nerves in the trunk develop in the regions of constriction between myelomeres. A comparison with the conditions in Amphioxus and Petromyzon shows that this condition is not to be regarded as primitive, but that previously dorsal and ventral nerves alternated, the former being intersomitic in position. Such topographical relation is retained by some cranial nerves, viz. V, VII, IX, and X (Urvagus).

The ganglionic Anlagen of four cranial nerves, viz. V, VII, IX, and X, are proliferated from four encephalomeres, viz. III, V, VI, and VII. Chiefly for this reason, but also because of the clear connection of two splanchnic motor roots, viz. V and VII, with two of the encephalomeres, I conclude that the primitive metameric relations of the latter were with the visceral arches. The local thickenings of the hindbrain neuromeres (encephalomeres) may be considered as the primitive nervous centres of nerves which corresponded numerically with visceral arches. If they were such, then one of the encephalomeres (IV) affords evidence of a lost visceral arch.

Although the structure of myelomeres and encephalomeres is seen to be different, yet in the stages of embryonic development, where both are present, the latter are seen to have segmental value from the fact that corresponding with them there is an equal number of somites. These somites, as exemplified in the 3d (van Wijhe's), are morphologically comparable and serially homologous with trunk somites. I conclude, then, that there was a primitive correspondence between neuromerism, mesomerism, and branchiomerism.

The development, histological structure, and relationships of the eye-muscle nerves (III, IV, and VI) show them to be the serial homologues of ventral spinal nerves. Like the latter (His), they develop as axis-cylinder processes of neuroblasts in the ventral horn of the neural tube.

Pre-otic and post-otic metameres, like their integral parts, are serially homologous with one another. Therefore, if the latter are serially homologous with trunk metameres the former must be also. Table III. (p. 253) summarizes my opinion as to the primitive composition of metameres I to VII. I regard the r. opthalmicus profundus as a segmental dorsal nerve belonging to metamere II, while the oculomotorius is its ventral root. The trochlearis is the ventral nerve of metamere III, and the abducens represents the ventral nerves of metameres IV to VII.

There are five mesomeres alternating with six neuromeres in the otic and pre-otic regions of the Vertebrate head. Probably eleven neuromeres are finally included in the head of Squalus. The evidence of the numerical correspondence of neuromeres and mesomeres shows that there is no more reason for believing that somites have been lost anterior to Platt's (anterior) somite, than that neuromeres have been lost anterior to the primary forebrain.

In agreement with van Wijhe, I homologize the mouth of Amphioxus with the left half of the mouth of Craniota. The first pair of permanent visceral clefts in Amphioxus are exactly homologous with the hyomandibular clefts of higher Vertebrates. The eight visceral clefts possessed by Amphioxus at its "critical stage" (Willey) are exactly homologous with the eight morphological clefts found in some Selachii and Cyclostomes.

This investigation has been made in the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College. I gratefully acknowledge the valuable assistance and advice of its Director, Prof. E. L. Mark, at whose suggestion the work was undertaken. I am indebted to Alexander Agassiz for the privilege of studying at his private laboratory in Newport; also to Professor Mark for embryonic material of Petromyzon, and to Miss Julia B. Platt for embryonic material of Amphioxus.

BIBLIOGRAPHY.

Ahlborn, F.
'84. Ueber den Ursprung und Austritt der Hirnnerven von Petromyzon. Zeitschr. f. wiss. Zool., Bd. 40, Heft 2, pp. 286–308, Taf. 18.

Ahlborn, F.
'84ª. Ueber die Segmentation des Wirbelthierkörpers. Zeitschr. f. wiss. Zool., Bd. 40, pp. 309–337.

Allis, E. P., Jr.
'89. The Anatomy and Development of the Lateral Line System in Amia calva. Jour. Morph., Vol. 2, pp. 463–566, Pls. 30–42.

Allis, E. P.
'97. The Cranial Muscles and Cranial and First Spinal Nerves in Amia calva. Jour. Morph., Vol. 12, pp. 487–808, Pls. 20–38.

Altmann, R.
'85. Bemerkungen zur Hensen'schen Hypothese von der Nervenentstehung. Arch. f. Anat. u. Phys., Jahrg. 1885, Anat. Abth., pp. 344–348, Taf. 14.

Ayers, H.
'92. Vertebrate Cephalogenesis. II. A Contribution to the Morphology of the Vertebrate Ear, with a Reconsideration of its Functions. Jour. Morph., Vol. 5, No. 1, pp. 1–360, Pls. 1–12.

Baer, K. E. von.
'28. Ueber Entwickelungsgeschichte der Thiere. Theil I. Königsberg, xxii + 271 pp., 3 Taf.

Balfour, F. M.
'78. A Monograph on the Development of Elasmobranch Fishes. London, xi + 295 pp., 20 Plates.

Balfour, F. M.
'81. A Treatise on Comparative Embryology. London. Vol. 2, xi + 655 + 22 pp., 429 Figs.

Beard, J.
'84. On the Segmental Sense Organs of the Lateral Line, and on the Morphology of the Vertebrate Auditory Organ. Zool. Anz., Jahrg. 7, pp. 123–126, 140–143.

Beard, J.

'85. The System of Branchial Sense Organs and their Associated Ganglia in Ichthyopsida. A Contribution to the Ancestral History of Vertebrates. Quart. Jour. Micr. Sci., Vol. 26, pp. 95–156, Pls. 8–10.

Beard, J.

'87. The Ciliary or Motoroculi Ganglion and the Ganglion of the Ophthalmicus profundus in Sharks. Anat. Anz., Jahrg. 2, No. 18 u. 19, pp. 565–575, 5 Figs.

Beard, J.

'88. Morphological Studies. II. The Development of the Peripheral Nervous System of Vertebrates. Quart. Jour. Micr. Sci., Vol. 29, pp. 153–227, Pls. 16–21.

Beard, J.

'92. The Histogenesis of Nerve. Anat. Anz., Jahrg. 7, pp. 290–302.

Béraneck, E.

'84. Recherches sur le développement des nerfs crâniens chez les Lézards. Recueil Zool. Suisse, Tom. 1, No. 4, pp. 519–603, Pls. 27–30.

Béraneck, E.

'87. Étude sur les replis médullaires du poulet. Recueil Zool. Suisse, Tom. 4, No. 2, pp. 305–364, Pl. 14.

Bischoff, T. L. W.

'42. Entwickelungsgeschichte der Säugethiere und des Menschen. Leipzig, xiv + 575 pp.

Broman, I.

'95. Beschreibung eines menschlichen Embryos von beinahe 3 mm. Länge mit spezieller Bemerkung über die bei demselben befindlichen Hirnfalten. Morph. Arbeiten, Bd. 5, Heft 2, pp. 169–206, Taf. 9, 10, u. 7 Textfig.

Burckhardt, R.

'93. Die Homologieen des Zwischenhirndaches und ihre Bedeutung für die Morphologie des Hirns bei niederen Vertebraten. Anat. Anz., Jahrg. 9, pp. 152–155. 1 Fig.

Burckhardt, R.

'94. Der Bauplan des Wirbelthiergehirns. Morph. Arbeiten, Bd. 4, Heft 2, pp. 131–150, Taf. 8.

Cajal, Ramon y.

'94. Les nouvelles idées sur la structure du systeme nerveux chez l'homme et chez les Vertébrés. Revue gen. sci. pures et appliquées, Anneé 5, pp. 141–153.

Chiarugi, G.

'91. Sur les myotomes et sur les nerfs de la tête postérieure et de la région proximale du tronc dans les embryons des Amphibies anoures. (Résumé.) Arch. Ital. de Biol., Tom. 15, fasc. II. pp. 229–239.

Chiarugi, G.
'94. Lo sviluppo dei nervi oculomotore e trigemello. Monitoire Zool. Ital., Anno V, No. 12, pp. 275–280.

Clarke, S. F.
'91. The Habits and Embryology of the American Alligator. Jour. Morph., Vol. 5, No. 2, pp. 181–214, Pl. 9–13.

Coggi, A.
'95. Il cordone gangliare anteriore in Torpedo e Pristiurus. Ricerche fati nel labor. anat. Univ. di Roma ed in altri labor. biolog., Vol. 5, pp. 27–41.

Dohrn, A.
'75. Der Ursprung der Wirbelthiere und das Princip des Functionswechsels. Genealogische Skizzen. Leipzig, xv + 87 pp.

Dohrn, A.
'85. Studien zur Urgeschichte des Wirbelthierkörpers. X. Zur Phylogenese des Wirbelthierauges. Mitth. Zool. Stat. Neapel, Bd. 6, Heft 3, pp. 432–480, Taf. 23, 24.

Dohrn, A.
'88. Studien u. s. w. XIII. Ueber Nerven und Gefässe bei Ammocoetes und Petromyzon Planeri. Mitth. Zool. Stat. Neapel, Bd. 8, Heft 2, pp. 231–306, Taf. 10–15.

Dohrn, A.
'90. Bemerkungen über den neuesten Versuch, einer Lösung des Wirbelthierkopf-Problems. Anat. Anz., Jahrg. 5, Hefte 2 u. 3, pp. 53–64, 78–85.

Dohrn, A.
'90ᵃ. Studien u. s. w. XV. Neue Grundlagen zur Beurtheilung der Metamerie des Kopfes. Mitth. Zool. Stat. Neapel, Bd. 9, Heft 3, pp. 330–434, Taf. 14, 15.

Dohrn, A.
'91. Studien u. s. w. XVI. Ueber die erste Anlage und Entwicklung der Augenmuskelnerven bei Selachiern und das Einwandern von Medullarzellen in die motorischen Nerven. Mitth. Zool. Stat. Neapel, Bd. 10, Heft 1, pp. 1–40, Taf. 1–5.

Dohrn, A.
'91ᵃ. Studien u. s. w. XVII. Nervenfaser und Ganglienzelle. Mitth. Zool. Stat. Neapel, Bd. 10, Heft 2, pp. 255–335, Taf. 16–23.

Dohrn, A.
'92. Die Schwann'schen Kerne der Selachierembryonen. Anat. Anz., Jahrg. 7, pp. 348–351.

Dursy, E.
'69. Zur Entwicklungsgeschichte des Kopfes des Menschen und der höheren Wirbelthiere. Tübingen, xii + 232 pp., und Atlas, 9 Taf.

Edinger, L.
'96. Vorlesungen über den Bau der nervösen Centralorgane des Menschen und der Thiere. 5^{te} Aufl., Leipzig, xii + 386 pp., 258 Abbildg.

Ewart, J. C.
'90. On the Development of the Ciliary or Motor Oculi Ganglion. Proc. Roy. Soc., London, Vol. 47, No. 289, pp. 287–290.

Eycleshymer, A. C.
'95. The early Development of Amblystoma, with Observations on some other Vertebrates. Jour. Morph., Vol. X. No. 2, pp. 343–418, Pls. 18–22.

Foster, M., and Balfour, F. M.
'74. The Elements of Embryology. London, xix + 272 pp., 71 Figs.

Froriep, A.
'85. Ueber Anlagen von Sinnesorganen am Facialis, Glossopharyngeus und Vagus, über die genetische Stellung des Vagus zum Hypoglossus, und über die Herkunft der Zungenmusculatur. Arch. f. Anat. u. Physiol., Anat. Abth., Jahrg. 1888, pp. 1–55, Taf. 1 u. 2.

Froriep, A.
'91. Zur Entwickelungsgeschichte der Kopfnerven. Verh. Anat. Gesellsch. V. (München), pp. 55–65.

Froriep, A.
'92. Zur Frage der sogenannten Neuromerie. Verh. Anat. Gesellsch. VI. (Wien), pp. 162–167.

Froriep, A.
'92ª. Entwickelungsgeschichte des Kopfes. Anat. Hefte, Abth. 2, Ergebnisse Anat. u. Entwg., Bd. 1, pp. 551–605.

Froriep, A.
'94. Entwickelungsgeschichte des Kopfes. Anat. Hefte, Abth. 2, Ergebnisse Anat. u. Entwg., Bd. 3, pp. 391–459.

Fürbringer, M.
'97. Ueber die Spino-occipitalen Nerven der Selachier und Holocephalen und ihre vergleichende Morphologie. Festschr. zum siebenzigsten Geb. von Carl Gegenbaur, Bd. 3, pp. 349–788, 8 Taf. Leipzig.

Fürbringer, P.
'75. Untersuchungen zur vergleichenden Anatomie der Muskulatur des Kopfskeletes der Cyclostomen. Jena. Zeitschr., Bd. 9, Heft 1, pp. 1–93, Taf. 1–3.

Gaskell, W. H.
'89. On the Relation between the Structure, Function, Distribution, and Origin of the Cranial Nerves; together with a Theory of the Origin of the Nervous System of Vertebrata. Jour. Phys., Vol. 10, No. 3, pp. 153–211, Pls. 16–20.

Gegenbaur, C.
'72. Untersuchungen zur vergleichenden Anatomie der Wirbelthiere. Heft 3. Das Kopfskelet der Selachier. Ein Beitrag zur Erkenntniss der Genese des Kopfskelets der Wirbelthiere. Leipzig, 10 + 316 pp., 22 Taf.

Gegenbaur, C.
'87. Die Metamerie des Kopfes und die Wirbeltheorie des Kopfskeletes. Morph. Jahrb., Bd. 13, Heft 1, pp. 1–114.

Goette, A.
'75. Die Entwickelungsgeschichte der Unke (Bombinator igneus) als Grundlage einer vergleichenden Morphologie der Wirbelthiere. Leipzig, viii + 964 pp., und Atlas (1874), 22 Taf. fol.

Goette, A.
'90. Entwickelungsgeschichte des Flussneunauges (Petromyzon fluviatilis). Theil I. Hamburg u. Leipzig, 95 pp., 9 Taf. Abhandl. z. Entwg. d. Thiere, Heft 5.

Golgi, C.
'93. Intorno all' origine del quarto nervo cerebralo (patetico o trocleare) e di una questione di Isto-fisiologia generale che a questo argomento si collega. Atti Accad. Lincei, Rendiconti, Vol. 2, Semestre 1, fasc. 9 e 10, pp. 379–389, 443–450, 2 Fig. *Also in French*, Arch. Ital. Biol., Tom. 19, fasc. 3, pp. 454–474.

Golowine, E.
'90. Sur le développement du système ganglionnaire chez le poulet. Anat. Anz., Jahrg. 5, No. 4, pp. 119–124, 4 Figg.

Goronowitsch, N.
'88. Das Gehirn und die Cranialnerven von Acipenser ruthenus. Ein Beitrag zur Morphologie des Wirbelthierkopfes. Morph. Jahrb., Bd. 13, Hefte 3 u. 4, pp. 427–574, Taf. 17–23.

Goronowitsch, N.
'92. Die axiale und die laterale (A. Goette) Kopfmetamerie der Vögelembryonen. Die Rolle der sog. "Ganglienleisten" im Aufbaue der Nervenstämme. Anat. Anz., Jahrg. 7, pp. 454–464.

Goronowitsch, N.
'93. Untersuchungen über die Entwicklung der sog. "Ganglienleisten" im Kopfe der Vögelembryonen. Morph. Jahrb., Bd. 20, Heft 2, pp. 187–259, Taf. 8–11.

Hatschek, B.
'81. Studien über Entwicklung des Amphioxus. Arb. Zool. Inst. Wien, Tom. 4, Heft 1, pp. 1–88, Taf. 1–9.

Hatschek, [B].
'92. Die Metamerie des Amphioxus und des Ammocoetes. Verh. Anat. Gesellsch. VI. (Wien), pp. 136–161, 11 Figg.

Hatschek, B.

'93. Zur Metamerie der Wirbelthiere. Anat. Anz., Jahrg 8, pp. 89–91.

Hensen, V.

'64. Zur Entwickelung des Nervensystems. Arch. f. Path. Anat. u. Phys., Bd. 30, pp. 176–186, Taf. 8.

Hensen, V.

'76. Beobachtungen über die Befruchtung und Entwicklung des Kaninchens und des Meerschweinschens Zeit. Anat. u. Entwg., Bd. 1, Hefte 3–6, pp. 213–273, 353–423, Taf. 8–12.

Herrick, C. L.

'92. Embryological Notes on the Brain of the Snake. Jour. Comp. Neurology, Vol. 2, pp. 160–176, Pl. 15–19.

His, W.

'79. Ueber die Anfänge des peripherischen Nervensystemes. Arch. f. Anat. u. Physiol., Anat. Abth., pp. 455–482, Pls. 17 u. 18.

His, W.

'88. Die Entwickelung der ersten Nervenbahnen beim menschlichen Embryo. Uebersichtliche Darstellung. Arch. f. Anat. u. Physiol., Anat. Abth., Heft 6, pp. 368–378, 8 Figg.

His, W.

'88ᵃ. Die morphologische Betrachtung der Kopfnerven. Eine kritische Studie. Arch. f. Anat. u. Physiol., Anat. Abth., Heft 6, pp. 379–453.

His, W.

'88ᵇ. Zur Geschichte des Gehirns, sowie der centralen und peripherischen Nervenbahnen beim menschlichen Embryo. Abhandl. Sächs. Gesellsch. Wissensch., math.-phys. Cl., Bd. 24, No. vii., pp. 341–392, Tab. 1 u. 2.

His, W.

'89. Die Neuroblasten und deren Entstehung im embryonalen Mark. Arch. f. Anat. u. Physiol., Anat. Abth., Hefte 3 u. 4, pp. 249–300, Taf. 16–19.

His, W.

'89ᵃ. Ueber die Entwickelung des Riechlappens und des Riechganglions und über diejenige des verlängerten Markes. Verh. Anat. Gesellsch. III. (Berlin), pp. 63–66.

Hoffmann, C. K.

'85. Weitere Untersuchungen zur Entwicklungsgeschichte der Reptilien. Morph. Jahrb., Bd. 11, Heft 2, pp. 176–219, Taf. 10–12, 1 Fig.

Hoffmann, C. K.

'89. Ueber die Metamerie des Nachirns und Hinterhirns, und ihre Beziehung zu den segmentalen Kopfnerven bei Reptilienembryonen. Zool. Anz., Jahrg. 12, pp. 337–339.

Hoffmann, C. K.

'90. Reptilien. V. Entwicklungsgeschichtlicher Theil. Bronn's Klassen und Ordnungen des Thier-Reichs, Bd. 6, Abth. 3, III. pp. 1872–1889, Taf. 138–170.

Hoffmann, C. K.
'94. Zur Entwickelungsgeschichte des Selachierkopfes. Anat. Anz., Bd. 9, pp. 638–653, 5 Figg.

Hoffmann, C. K.
'96. Beiträge zur Entwickelungsgeschichte der Selachii. Morph. Jahrb., Bd. 24, Heft 2, pp. 209–286, Taf. 2–5.

Houssay, F.
'90. Études d'embryologie sur les Vertébrés. Arch. de Zool. exp. et gen., sér. 2, Tom. 8, No. 2, pp. 143–244, Pls. 10–13. [II. Origine et développement du système nerveux périferique. pp. 178–208.]

Houssay, F.
'91. Études d'embryologie sur les Vertébrés. IV. Les fentes branchiales auditive, hyo-mandibulaire, spiraculaire et les somites mésoblastiques qui leur correspondent chez l'Axolotl. Bull. Sci. de la France et de la Belgique, Tom. 23, Pt. 1, pp. 55–71, Pls. 1–3.

Huxley, T. H.
'58. The Croonian Lecture. — On the Theory of the Vertebrate Skull. Proc. Roy. Soc. Lond., Vol. 9, No. 33, pp. 381–457, 10 Figs.

Kastschenko, N.
'88. Zur Entwicklungsgeschichte des Selachierembryos. Anat. Anz., Jahrg. 3, No. 16, pp. 445–467.

Killian, [G.]
'91. Zur Metamerie des Selachierkopfes. Verh. Anat. Gesellsch. V. (München), pp. 85–107, 25 Figg.

Kölliker, A.
'61. Entwicklungsgeschichte des Menschen und der höheren Thiere. Leipzig, x + 468 pp., 225 Figg.

Kölliker, A.
'79. Entwicklungsgeschichte des Menschen und der höheren Thiere. 2te Aufl. Leipzig, xxxiv + 1033 pp., 606 Figg.

Kölliker, [A.]
'92. Ueber die Entwickelung der Elemente des Nervensystems, contra Beard und Dohrn. Verh. Anat. Gesellsch. VI. (Wien), pp. 76–78.

Krause, W.
'81. Ueber die doppelnatur des Ganglion ciliare. Morph. Jahrb., Bd. 7, Heft 1, pp. 43–56, Taf. 5.

Kupffer, C.
'86. Primäre Metamerie des Neuralrohrs der Vertebraten. Sitzb. Akad. Wissensch. München, math.-phys. Cl., 1885, Heft 4, pp. 469–476.

Kupffer, C.
'88. Ueber die Entwicklung von Petromyzon Planeri. Sitzb. Akad. Wissensch. München, Bd. 18, Heft 1, pp. 71–79.

Kupffer, C.
'90. Die Entwicklung von Petromyzon Planeri. Arch. f. mikr. Anat., Bd. 35, Heft 4, pp. 469–558, Taf. 27–32.

Kupffer, C.
'91. Die Entwickelung der Kopfnerven der Vertebraten. Verh. Anat. Gesellsch. V. (München), pp. 22–55.

Kupffer, C.
'93. Die Entwicklung des Kopfes von Acipenser sturio, an Medianschnitten untersucht. Studien zur vergleichenden Entwicklungsgeschichte des Kopfes der Kranioten. Heft 1. München und Leipzig, iv + 95 pp., 9 Taf.

Kupffer, C.
'93ª. Entwickelungsgeschichte des Kopfes. Anat. Hefte, Abth. 2. Ergebnisse Anat. u. Entwg., Bd. 2, pp. 501–564.

Kupffer, C.
'94. Die Entwicklung des Kopfes von Ammocoetes Planeri. Studien z. vergl. Entwg. d. Kopfes d. Kranioten, Heft 2. München und Leipzig, 79 pp., 12 Taf.

Kupffer, C.
'95. Die Entwicklung der Kopfnerven von Ammocoetes Planeri. Studien z. vergl. Entwg. d. Kopfes d. Kranioten, Heft 3. München, J. F. Lehmann, 1895.

Kupffer, C.
'96. Entwickelungsgeschichte des Kopfes. Anat. Hefte, Abth. 2, Ergebnisse Anat. u. Entwg., Bd. 5, pp. 562–618, 4 Abbildg.

Lenhossék, M. von.
'90. Ueber Nervenfasern in den hinteren Wurzeln, welche aus dem Vorderhorn entspringen. Anat. Anz., Jahrg. 5, No. 13 u. 14, pp. 360–362.

Lenhossék, M. von.
'91. Die Entwickelung der Ganglionanlagen bei dem menschlichen Embryo. Arch. f. Anat. u. Physiol., Anat. Abth., Heft 1, pp. 1–25, Taf. 1.

Lenhossék, M. von.
'92. Beobachtungen an den Spinalganglien und dem Rückenmark von Pristiurusembryonen. Anat. Anz., Jahrg. 7, pp. 519–539, 19 Abbildg.

Locy, W. A.
'93. The Derivation of the Pineal Eye. Anat. Anz., Bd. 9, No. 5 u. 6, pp. 169–180, 5 Figs.

Locy, W. A.
'94. The Optic Vesicles of Elasmobranchs and their Serial Relation to other Structures on the Cephalic Plate. Jour. Morph., Vol. 9, pp. 115–122.

[Locy, W. A.]
'94^{a}. Nachtrag zu dem Aufsatze von Locy in No. 5 und 6, p. 169. Anat. Anz., Bd. 9, No. 7, pp. 231, 232.

Locy, W. A.
'94^{b}. Metameric Segmentation in the Medullary Folds and Embryonic Rim. Anat. Anz., Bd. 9, No. 13, pp. 393–415, 11 Figs.

Locy, W. A.
'94^{c}. The Mid-Brain and Accessory Optic Vesicles. A Correction. Anat. Anz., Bd. 9, No. 15, pp. 486–488.

Locy, W. A.
'95. Contribution to the Structure and Development of the Vertebrate Head. Jour. Morph., Vol. 11, No. 3, pp. 497–594, Pls. 26–30.

Locy, W. A.
'97. Accessory Optic Vesicles in the Chick Embryo. Anat. Anz., Bd. 14, No. 5, pp. 113–124, 9 Figs.

Marshall, A. M.
'78. The Development of the Cranial Nerves of the Chick. Quart. Jour. Micr. Sci., Vol. 18, No. 69, pp. 10–40, Pls. 2, 3.

Marshall, A. M.
'81. On the Head Cavities and Associated Nerves in Elasmobranchs. Quart. Jour. Micr. Sci., Vol. 21, pp. 72–97, Pls. 5, 6.

Marshall, A. M.
'82. The Segmental Value of the Cranial Nerves. Jour. Anat. Physiol., Vol. 16, Pt. 3, pp. 305–354, Pl. 10. Also in Stud. Biol. Lab., Owens College, Vol. 1, pp. 125–169. 1886.

Marshall, A. M.
'93. Vertebrate Embryology. New York and London. xxiii + 640 pp., 255 Figs.

Marshall, A. M., and Spencer, W. B.
'81. Observations on the Cranial Nerves of Scyllium. Quart. Jour. Micr. Sci., Vol. 21, No. 82, pp. 469–499, Pl. 27. Also in Stud. Biol. Lab., Owens College, Vol. 1, pp. 87–123, Pls. 5, 6. 1886.

Martin, P.
'90. Die erste Entwickelung der Kopfnerven der Katze. Oesterr. Monatsschr. f. Thierheilkunde, Jahrg. 15. Sept., 1890.

Martin, P.
'91. Die Entwickelung der neunten bis zwölften Kopfnerven bei der Katze. Anat. Anz., Jahrg. 6, Heft 8, pp. 228–232.

McClure, C. F. W.
'89. The Primitive Segmentation of the Vertebrate Brain. Zool. Anz., Jahrg. 12, No. 314, pp. 435–438.

McClure, C. F. W.
'90. The Segmentation of the Primitive Vertebrate Brain. Jour. Morph., Vol. 4, pp. 35–56, Pl. 3.

Mihalkovics, V. von.
'77. Entwicklungsgeschichte des Gehrins. Leipzig, 203 pp., 7 Taf.

Minot, C. S.
'92. Human Embryology. New York. xxiii + 815 pp., 463 Figs. [pp. 604–606.]

Minot, C. S.
'97. Cephalic Homologies. A Contribution to the Determination of the Ancestry of Vertebrates. Amer. Nat., Vol. 31, No. 371, pp. 927–943.

Mitrophanow, P.
'91. Sur la formation du système nerveux périférique des Vertébrés. Comptes Rendus, Paris, Tom. 113, No. 19, pp. 659–662.

Mitrophanow, P.
'92. Note sur la signification metamerique des nerfs crâniens. Congrès Internat. de Zool., Session 2, Moscou, Partie 1, pp. 104–111.

Mitrophanow, P.
'93. Étude embryogénique sur les Sélaciens. Arch. Zool. exp., sér. 3, Tom. 1, pp. 161–220, Pls. 9–14.

Neal, H. V.
'96. A Summary of Studies on the Segmentation of the Nervous System in Squalus acanthias. Anat. Anz., Bd. 12, No. 17, pp. 377–391, 6 Figs.

Neal, H. V.
'97. The Development of the Hypoglossus Musculature in Petromyzon and Squalus. Anat. Anz., Bd. 13, No. 17, pp. 441–463, 2 Figs.

Ónodi, A. D.
'84. Ueber die Entwickelung der Spinalganglien und der Nervenwurzeln. Internat. Monatschr. f. Anat. u. Histol., Bd. 1, pp. 204–209, 255–284.

Oppel, A.
'90. Ueber Vorderkopfsomiten und die Kopfhöhle bei Anguis fragilis. Arch. f. mikr. Anat., Bd. 36, pp. 603–627, Taf. 30.

Orr, H. B.
'87. Contribution to the Embryology of the Lizard. Jour. Morph., Vol. 1, pp. 311–372, Pls. 12–14.

Pinkus, F.
'94. Ueber einen noch nicht beschriebenen Hirnnerven des Protopterus annectens. Anat. Anz., Bd. 9, No. 18, pp. 562–566, 4 Fig.

Platt, J. B.
'89. Studies on the Primitive Axial Segmentation of the Chick. Bull. Mus Comp. Zoöl. Harvard Coll., Vol. 17, No. 4, pp. 171–190, 2 Pls.

Platt, J. B.

'91. A Contribution to the Morphology of the Vertebrate Head, based on a Study of Acanthias vulgaris. Jour. Morph., Vol. 5, pp. 79–112, Pls. 4–6.

Platt, J. B.

'91ª. Further Contribution to the Morphology of the Vertebrate Head. Anat. Anz., Jahrg. 6, No. 9 u. 10, pp. 251–265, 15 Figs.

Platt, J. B.

'93. Ectodermic Origin of the Cartilages of the Head. Anat. Anz. Jahrg. 8, No. 14 u. 15, pp. 506–509.

Platt, J. B.

'94. Ontogenetische Differenzirung des Ectoderms in Necturus. Studie I. Archiv. f. mikr. Anat., Bd. 43, Heft 4, pp. 911–966, Taf. 37–42.

Platt, J. B.

'96. Ontogenetic Differentiation of the Ectoderm in Necturus. Study II. On the Development of the Peripheral Nervous System. Quart. Jour. Micr. Sci., Vol. 38, pp. 485–547, Pls. 36–38.

Platt, J. B.

'97. The Development of the Cartilaginous Skull, and of the Branchial and Hypoglossal Musculature in Necturus. Morph. Jahrb., Bd. 25, Heft 3, pp. 377–464, Taf. 16–18.

Pollard, H. B.

'95. Ueber Labialknorpel. Verh. Anat. Gesellsch. IX. (Basel), pp. 232–235, 3 Abbildg.

Prenant, A.

'89. Note sur l'existence des replis médullaires chez l'embryon du porc. Bull. Soc. Sci. Nancy, sér. 2, Tom. 9, fasc. 22, pp. 84–93, 1 Pl.

Price, G. C.

'96. Zur Ontogenie eines Myxinoiden (Bdellostoma Stouti, Lockington). Sitzb. Akad. Wissensch. München, math.-phys. Cl., Bd. 26, Heft 1, pp. 69–74.

Price, G. C.

'96ª Some Points in the Development of a Myxinoid (Bdellostoma Stouti Lockington). Verh. Anat. Gesellsch. X. (Berlin), pp. 81–86.

Rabl, C.

'85. Bemerkung über die Segmentirung des Hirnes. Zool. Anz., Jahrg. 8, No. 191, pp. 192, 193.

Rabl, C.

'87. Ueber das Gebiet des Nervus facialis. Anat. Anz., Jahrg. 2, No. 8, pp. 219–227.

Rabl, C.

'89. Theorie des Mesoderms. Morph. Jahrb., Bd. 15, Heft 2, pp. 113–252, Taf. 7–9, u. 9 Figs.

Rabl, [C.]
'92. Ueber die Metamerie des Wirbeltierkopfes. Verh. Anat. Gesellsch. VI. (Wien), pp. 104–135, Taf. 2, u. 4 Abbildg.

Ramon y Cajal. See **Cajal, Ramon y.**

Ransom, W. B., and Thompson, D'A. W.
'86. On the Spinal and Visceral Nerves of Cyclostomata. Zool. Anz., Jahrg. 9, pp. 421–426.

Remak, R.
'55. Untersuchungen über die Entwickelung der Wirbelthiere. Berlin, fol. 194 + xxxviii. pp., 12 Taf.

Retzius, G.
'94. Ueber das Ganglion ciliare. Anat. Anz., Bd. 9, No. 21, pp. 633–637, 2 Abbildg.

Sagemehl, M.
'82. Untersuchungen über die Entwickelung der Spinalnerven. (Diss.) Dorpat, 47 pp., 2 Taf.

Sagemehl, M.
'83. Beiträge zur vergleichenden Anatomie der Fische. I. Das Cranium von Amia calva L. Morph. Jahrb., Bd. 9, Heft 2, pp. 177–228, Taf. 10.

Schneider, A.
'79. Beiträge zur vergleichenden Anatomie und Entwicklungsgeschichte der Wirbelthiere. Berlin, viii + 164 pp., 16 Taf., 3 Holzschn.

Schneider, A.
'80. Ueber die Nerven von Amphioxus, Ammocoetes und Petromyzon. Zool. Anz., Jahrg. 3, No. 59, pp. 330–334.

Schwalbe, G.
'79. Das Ganglion oculomotorii. Ein Beitrag zur vergleichenden Anatomie der Kopfnerven. Jena. Zeitschr., Bd. 13, pp. 173–268, Taf. 12–14.

Scott, W. B.
'87. Notes on the Development of Petromyzon. Jour. Morph., Vol. 1, No. 2, pp. 253–310, Pls. 8–11.

Sedgwick, A.
'92. Notes on Elasmobranch Development. Quart. Jour. Micr. Sci., Vol. 33, Pt. 4, pp. 559–586, Pl. 35.

Sedgwick, A.
'94. On the Inadequacy of the Cellular Theory of Development, and on the Early Development of Nerves, particularly of the Third Nerve and of the Sympathetic in Elasmobranchii. Quart. Jour. Micr. Sci., Vol. 37, pp. 87–101.

Sewertzoff, A. [N.]
'95. Die Entwickelung der Occipitalregion der niederen Vertebraten im Zusammenhang mit der Frage über die Metamerie des Kopfes. Bull. Soc. Imp. Nat. Moscou, Année 1895, No. 2, pp. 186–284, Pl. 4 et 5.

Sewertzoff, A. N.
'98. Die Metamerie des Kopfes von Torpedo. Anat. Anz., Bd. 14, No. 10, pp. 278–282.

Shipley, A. E.
'87. On some Points in the Development of Petromyzon fluviatilis. Quart. Jour. Micr. Sci., Vol. 27, pp. 325–370, Pl. 26–29.

Stannius, H.
'49. Das peripherische Nervensystem der Fische, anatomisch und physiologisch untersucht. Rostock, iv + 156 pp., 5 Taf.

Strong, O. S.
'95. The Cranial Nerves of Amphibia. Jour. Morph., Vol. 10, No. 1, pp. 101–230, Pls. 7–12.

Waters, B. H.
'91. Some additional Points on the Primitive Segmentation of the Vertebrate Brain. Zool. Anz., Jahrg. 14, No. 362, pp. 141–144.

Waters, B. H.
'92. Primitive Segmentation of the Vertebrate Brain. Quart. Jour. Micr. Sci., Vol. 33, Pt. 4, pp. 457–475, Pl. 28.

Wiedersheim, R.
'80. Das Gehirn von Ammocoetes und Petromyzon Planeri mit besonderer Berücksichtigung der spindlartigen Hirnnerven. Morph. Studien, Heft 1, pp. 3–26. Jena.

Weedersheim, R.
'92. "Discussion" *in* Verhandl. Anat. Gesellsch., VI. (Wien), p. 167.

Wiedersheim, R.
'93. Grundriss der vergleichenden Anatomie der Wirbelthiere. Aufl. 3, Jena, xx + 695 pp., 387 Figg., 4 Taf.

Wijhe, J. W. van.
'82. Ueber die Mesodermsegmente und die Entwickelung der Nerven der Selachierkopfes. Natuurk. Verh. d. K. Akad. Wissensch. Amsterdam, Deel 22, 50 pp., 5 Taf., 1883. Also separate, Amsterdam, 1882, 50 pp., 5 Taf.

Wijhe, J. W. van.
'86. Ueber Somiten und Nerven im Kopfe von Vögel- und Reptilienembryonen. Zool. Anz., Jahrg. 9, No. 237, pp. 657–660.

Wijhe, J. W. van.
'86a. Ueber die Kopfsegmente und die Phylogenie des Geruchsorganes der Wirbelthiere. Zool. Anz., Jahrg. 9, No. 238, pp. 678–682.

Wijhe, J. W. van.
'89. Die Kopfregion der Kranioten beim Amphioxus, nebst Bemerkungen über die Wirbeltheorie des Schädels. Anat. Anz., Jahrg. 4, No. 18, pp. 558–566.

Wijhe, J. W. van.

'93. Ueber Amphioxus. Anat. Anz., Jahrg. 8, No. 5, pp. 152–172.

Wilder, B. G.

'89. The Gross Anatomy of the Brain. Wood's Reference Handbook of the Medical Sciences, Vol. 8, pp. 107–164.

Willey, A.

'94. Amphioxus and the Ancestry of the Vertebrates. Macmillan & Co., New York and London. xiv + 316 pp, 135 Text Figures.

Zimmermann, W.

'91. Ueber die Metamerie des Wirbelthierkopfes. Verh. Anat. Gesellsch., V. (München), pp. 107–113.

Zimmermann, W.

'93. [Demonstration of a reconstruction drawing of abducens, ventral roots of glossopharyngeus and vagus, and of the hypoglossus in a human embryo in the beginning of the second month.] Verh. Anat. Gesellsch. VII. (Göttingen), p. 216.

DESCRIPTION OF PLATES.

All the drawings were made with the Abbé camera lucida. Figure 40 (Plate **6**) is, however, a reconstruction from sections and dissected specimens. The Figures of Plates **8** and **9**, with the exception of Figures 61 and 65, are also reconstructions from several sections. In sagittal sections, the embryo is always viewed from the right side. In cross sections, it is the posterior face of the section that is shown, so that right in the figure corresponds to right in the section. In frontal sections, the dorsal face is shown, so that right in the figure here also corresponds with right in the section. Only Figures 2 and 3 (Plate **1**) represent embryos viewed from the ventral side, so that what appears on the left side in these two figures is really on the right side of the embryo. The cells of the neural crest are in all cases colored blue.

ABBREVIATIONS COMMON TO ALL FIGURES OF TEXT AND PLATES.

*	Posterior limit of cephalic plate.
I–VII.	Encephalomeres.
1–7.	Somites (van Wijhe's).
2′, 3′.	Cavities of head somites 2, 3.
V. md.	Ramus mandibularis trigemini.
V. mx.	R. maxillaris trigemini.
V. opt. su.	R. ophth. superficialis trigemini.
V. opt. p'fnd.	R. opth. profundus trig.
V. rx. maj.	Radix major trigemini.
V. rx. min.	" minor trigemini.
VII. ac.	Ramus acusticus facialis.
VII. buc.	" buccalis "
VII. hoi.	" hyoideus "
VII. opt. su.	" ophth. superficialis fac.
α, β, γ.	Position of frontal sections (Figs. 36, 37, 38).
αβ.	(Fig. C.) Position of section (Fig. D).
a.	" Anterior cavity " (Figs. B, C, E). Ventral fibre tract (Fig. F).
abd.	Abducens nerve.
ao. d.	Dorsal aorta.
arc. vsc. 1.	Visceral arch 1.
ar'ent.	Archenteron.
au.	Auditory invagination (otic vesicle).
ax-cyl.	Axis-cylinder process.
brs. vsc. 1–6.	Visceral pouches 1 to 6.
cav. a.	Platt's somite (anterior cavity).
cbl.	Anlage of cerebellum.
cd.	Chorda dorsalis.
cl. crs. n.	Neural-crest cells.
cl. ms-ce.	Cells of mesocephalic ganglion.
cl. n'bl.	Neuroblastic cell.
coms. a.	Anterior commissure.
coms. d.	Dorsal "
coms. p.	Posterior commissure.
coms. su.	Superior "
ec'drm.	Ectoderm.
en'drm.	Entoderm.
ent.	Entoderm.
fis. vsc. 1–6.	Visceral clefts 1 to 6.
gls-phy.	Glossopharyngeus nerve.
gn. ac-fac.	Ganglionic Anlage of acustico-facialis.
gn. fac.	Ganglion of acustico-facialis.
gn. Gas.	Gasserian ganglion.
gn. gls-phy.	Ganglion of glossopharyngeus.
gn. ms-ce.	Mesocephalic ganglion.
gn. trig.	Ganglionic Anlage of the trigeminus nerve.
gn. spi.	Spinal ganglion.
gn. vag.	Ganglionic Anlage of the Vagus.
i'fb.	Infundibulum.
la. ct.	Lamina cutis (cutis plate).
la. mu.	Lamina muscularis (muscle plate).
m-b.	Midbrain.
mu. ob. su.	Superior oblique muscle.
mu. rt. su.	" rectus muscle.
mu. rt. a.	Anterior rectus muscle.
my'cœl.	Myocœle.
myl-mer.	Myelomere.
my-tm.	Myotome.
n-po.	Neuropore.
oc-mot.	Oculomotorius nerve.
pr'enc.	Prosencephalon.
rx. v.	Ventral root of nerve.
so.	Somite.
tb. n.	Neural tube.
thl.	Thalamic portion of the trigeminus Anlage.
trch.	Trochlearis nerve.
vag.	Vagus nerve.
vn. crd.	Vena cardinalis.
vs. opt.	Optic vesicle.

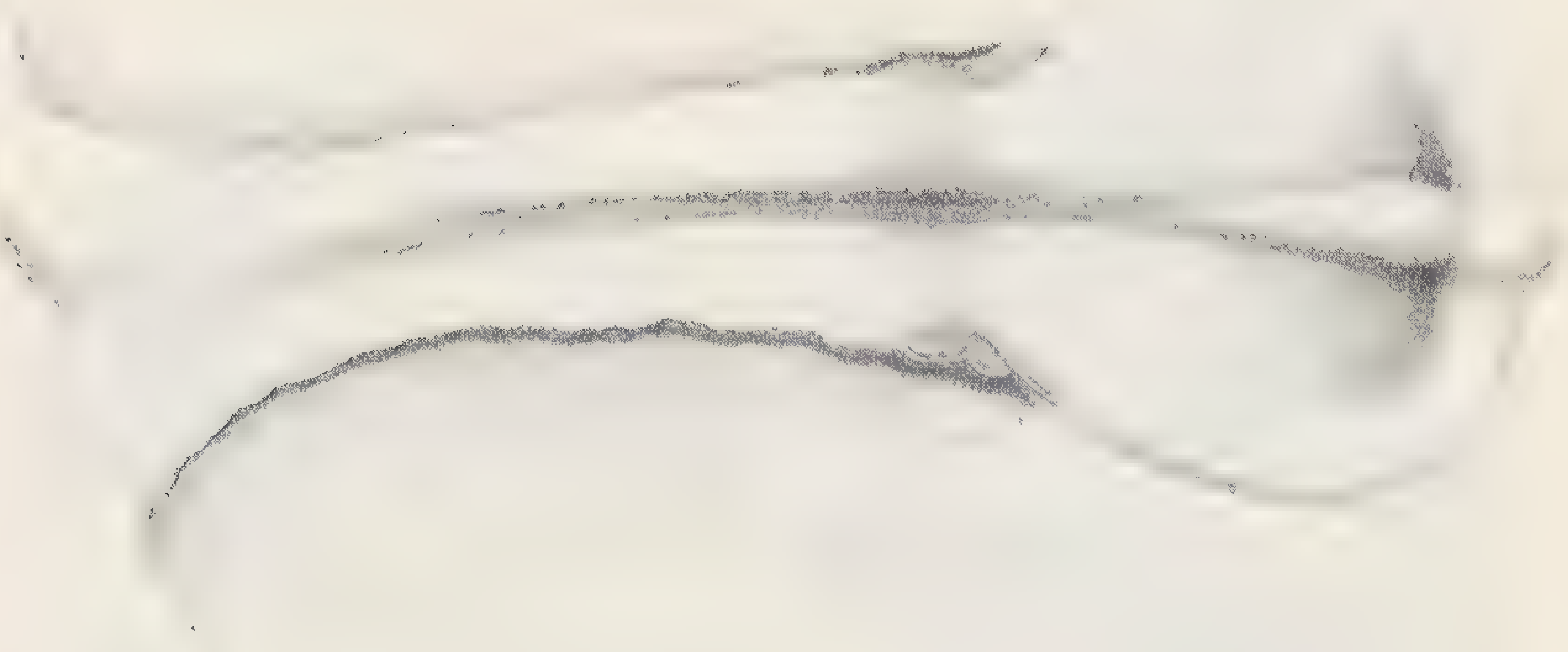
PLATE 1.

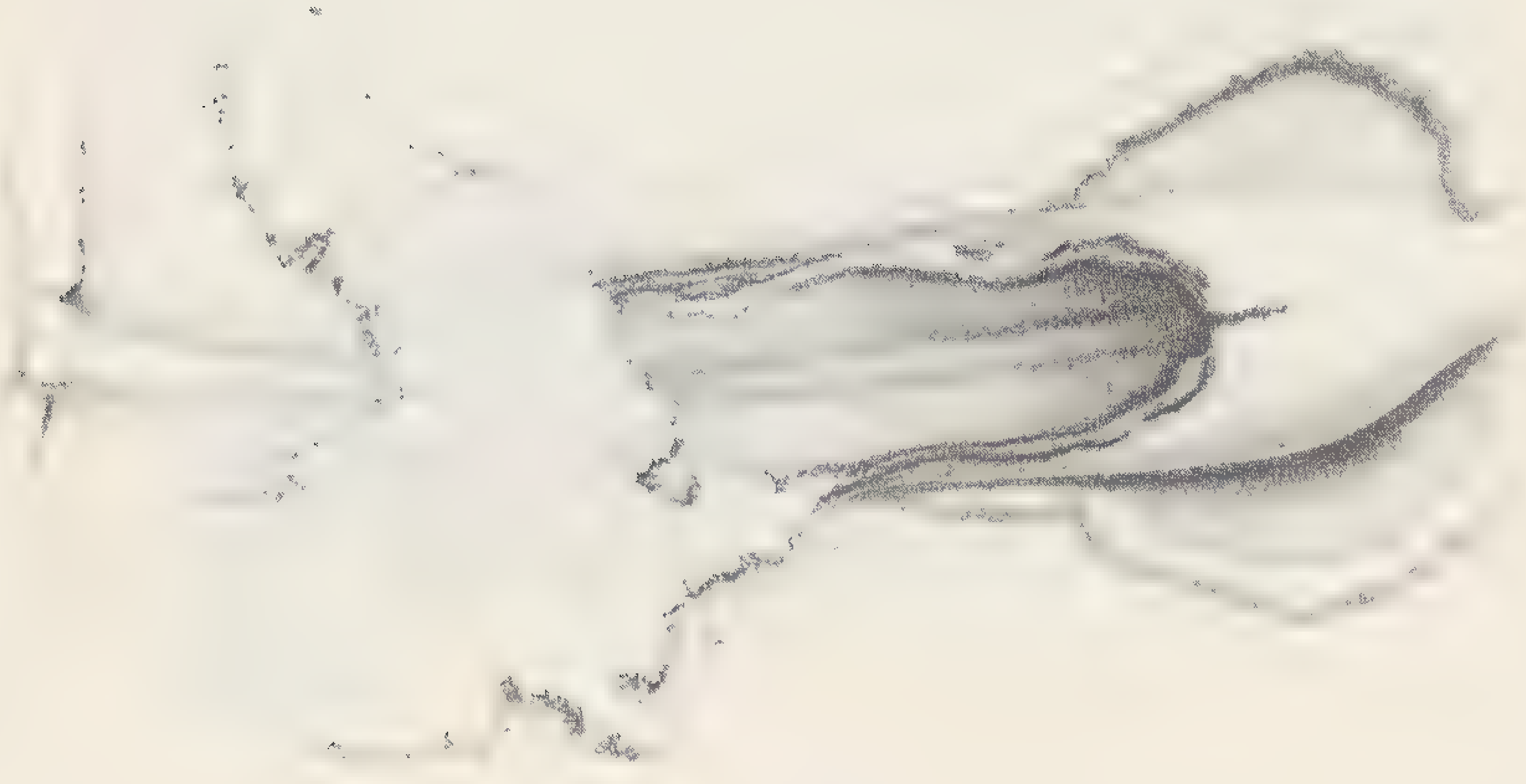
All figures magnified 43 diameters, and oriented on the plate with the chief axis horizontal, the anterior end of the embryo to the right. The embryo made translucent was drawn in outline with camera lucida and afterwards studied as an opaque object.

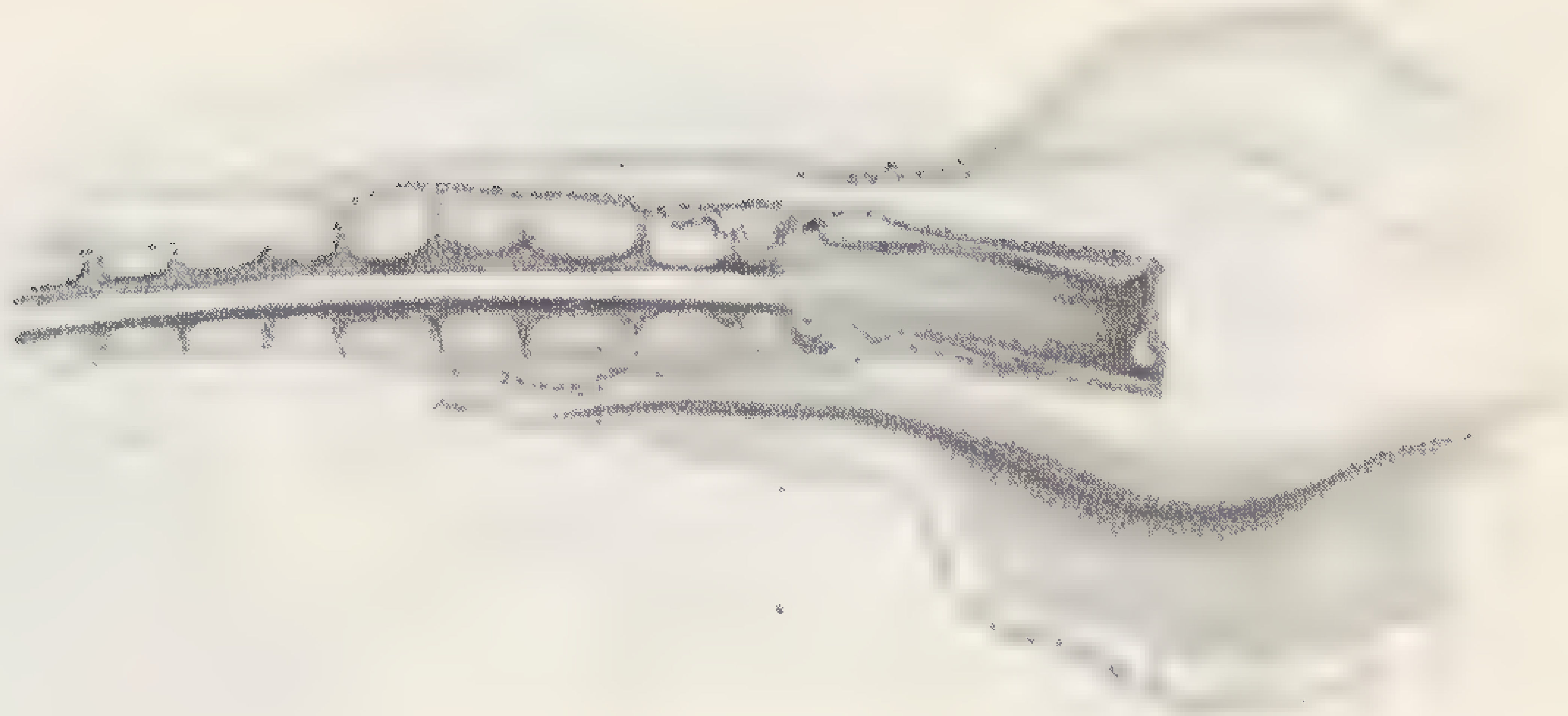
Fig. 1. A dorsal view of an embryo with 6 to 6½ somites. The edges of the neural plate are seen to be irregularly lobed. The two deep depressions at the anterior end of the cephalic plate mark the position of the future fundus of the infundibulum.

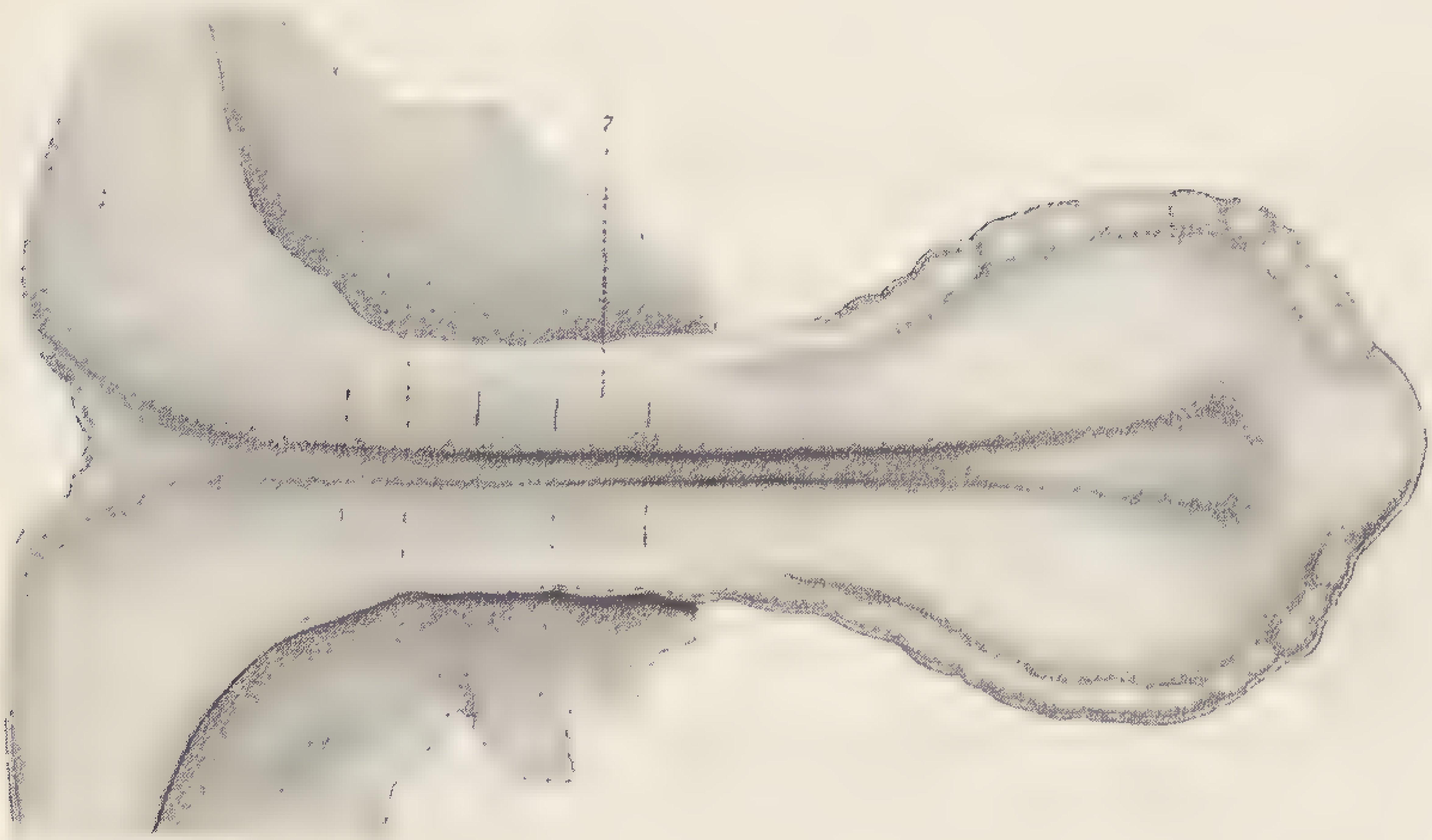
Fig. 2. A ventral view of the same embryo. Locy's segments are seen as lobings of the ventrally recurved margin of the neural plate.

Fig. 3. A ventral view of another embryo of the same stage of development. The specimen was dissected to show the chorda, a rod in the median axial line, on either side of which lie the somites, van Wijhe's seventh somite being designated as 7. An asterisk (*) marks the posterior boundary of the cephalic plate.

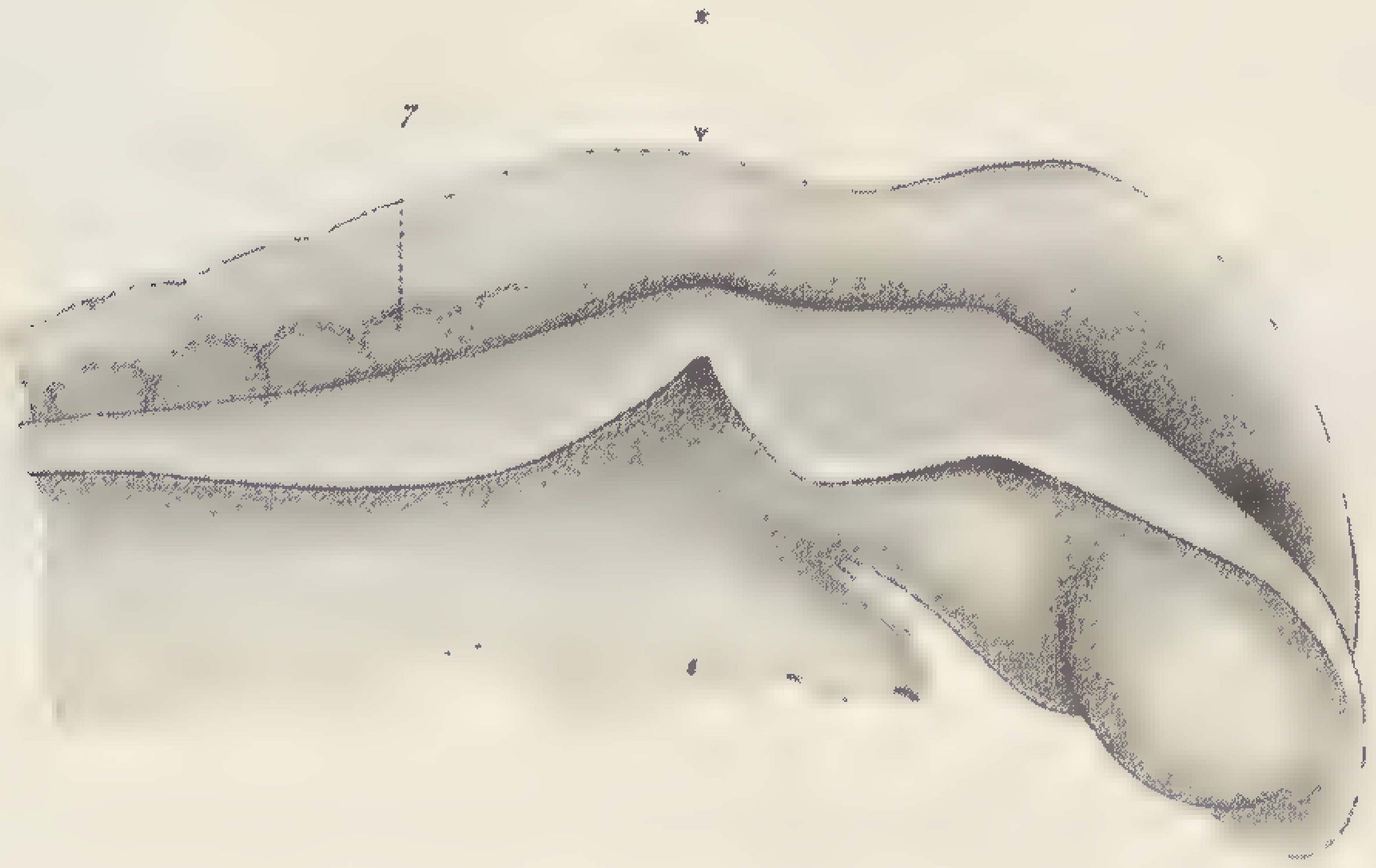




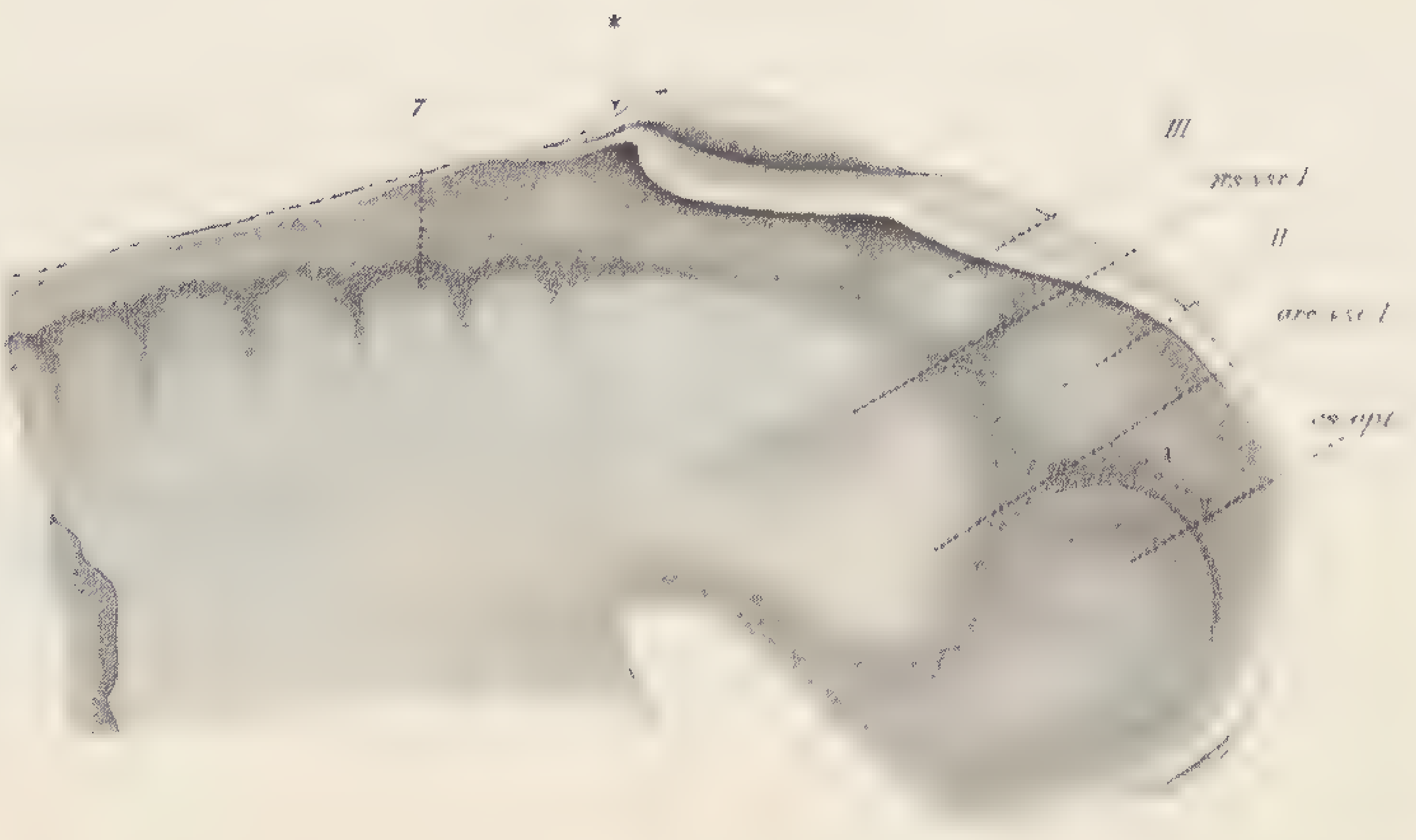




4



5


*
7
v
III
ms vsc I
II
arc vsc I
os opt

6

PLATE 2.

All figures magnified 43 diameters and oriented as in Plate 1. The outlines were first made from the translucent embryos with camera lucida, and afterwards the embryos were studied as opaque objects.

Fig. 4. An embryo with 4 somites viewed from the dorsal side. Locy's segments are seen to be confined to the "marginal bands" of the cephalic plate.

Fig. 5. An embryo with 10 or 11 somites viewed from the right side and partly from above. The posterior part of the cephalic plate is seen to be sharply flexed ventrad on the right side.

Fig. 6. An embryo with 12 somites viewed from the right side. The neural folds in the region of the cephalic plate have not yet met in the mid-dorsal line. The demarcation between cephalic plate and trunk is seen to be sharp. The anterior three primary vesicles (encephalomeres I, II, and III) appear in surface study as shown in the figure. In neither this embryo nor in the one represented in Figure 5 do Locy's segments appear.

PLATE 3.

All figures drawn from cleared specimens and magnified 43 diameters. The neural tube seen in optical sagittal section. Neural-crest cells (ganglionic Anlagen) colored in blue. In all cases the embryo is viewed from the right side.

Fig. 7. An embryo with 14 to 16 somites. Six vesicles only appear, and these are included within the limits of the cephalic plate. Neural crest (trigeminus Anlage) differentiated in the region of encephalomeres II and III. The mesodermic constrictions dividing somites 1, 2, 3, and 4 have appeared. Two visceral pouches (1 and 2) are in the process of breaking through the lateral plates (splanchnic mesoderm).

Fig. 8. Embryo with 18 or 19 somites. A thickening of the lateral zones in the posterior part of encephalomere III (not shown in figure) appears in sections of this stage. The acustico-facialis Anlage has become differentiated in the region of encephalomere V. The "anterior cavity" (Platt's) begins to be cut off from the mesoderm of the 1st somite (van Wijhe's).

Fig. 9. Embryo with 19 or 20 somites. A dorsal expansion now appears behind VI, as the first indication of encephalomere VII. Posteriorly it is bounded by somite 6. The constriction between van Wijhe's 3d and 4th somites has become obscured by the migration of cells from both sides of the constriction to meet the advancing Anlage of the acustico-facialis.

Fig. 10. Embryo with 21 or 22 somites. The conditions remain practically unchanged.

Fig. 11. Embryo with 24 or 25 somites. A ventral migration of neural-crest cells in the region of encephalomere VI has now begun, and the crest is now differentiated in the region of encephalomere VII and posteriorly.

Fig. 12. Embryo with 26 or 27 somites. A continuous neural crest extends from encephalomere V into the trunk region. Thalamic portion of the trigeminus Anlage clearly differentiated.

Fig. 13. Embryo with 28 to 30 somites. At this stage all of van Wijhe's somites appear clearly differentiated. The Anlagen of the acustico-facialis and the glossopharyngeus, differentiated from encephalomeres V and VI, appear topographically related to the constrictions between van Wijhe's somites, 3–4 and 4–5.

Fig. 14. Embryo with 33 or 34 somites. Trochlear portion of trigeminus Anlage (compare Fig. 21, *trch.*) clearly differentiated. The commissure connecting acustico-facialis and glossopharyngeus appears dorsal to the auditory invagination.

Fig. 15. Embryo with 38 or 39 somites.

Fig. 16. Embryo with 42 somites. Platt's "anterior somite" (*cap. a.*) clearly differentiated. The anterior cells of the vagus Anlage, proliferated from encephalomere VII, have become clearly differentiated in the 3d visceral arch as the Urvagus Anlage. Two visceral clefts have appeared.

Fig. 17. Embryo with 48 somites (7.5 mm.). The fifth and seventh nerves have assumed fibrillar relation with the neural tube. The main branches of the trigeminus begin to appear.

PLATE 4.

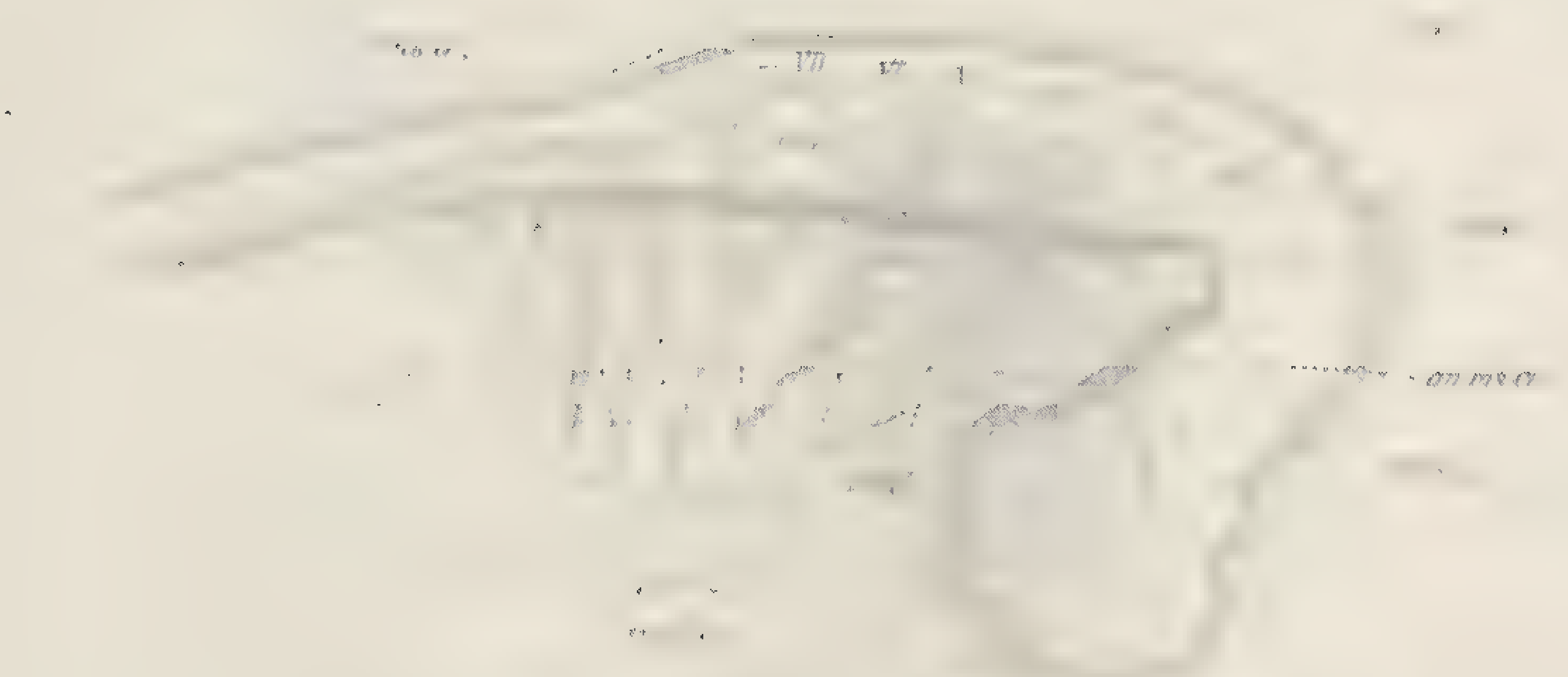
Figs. 18 and 21 magnified 23 diameters. Figs. 19 and 20 magnified 21 diameters.

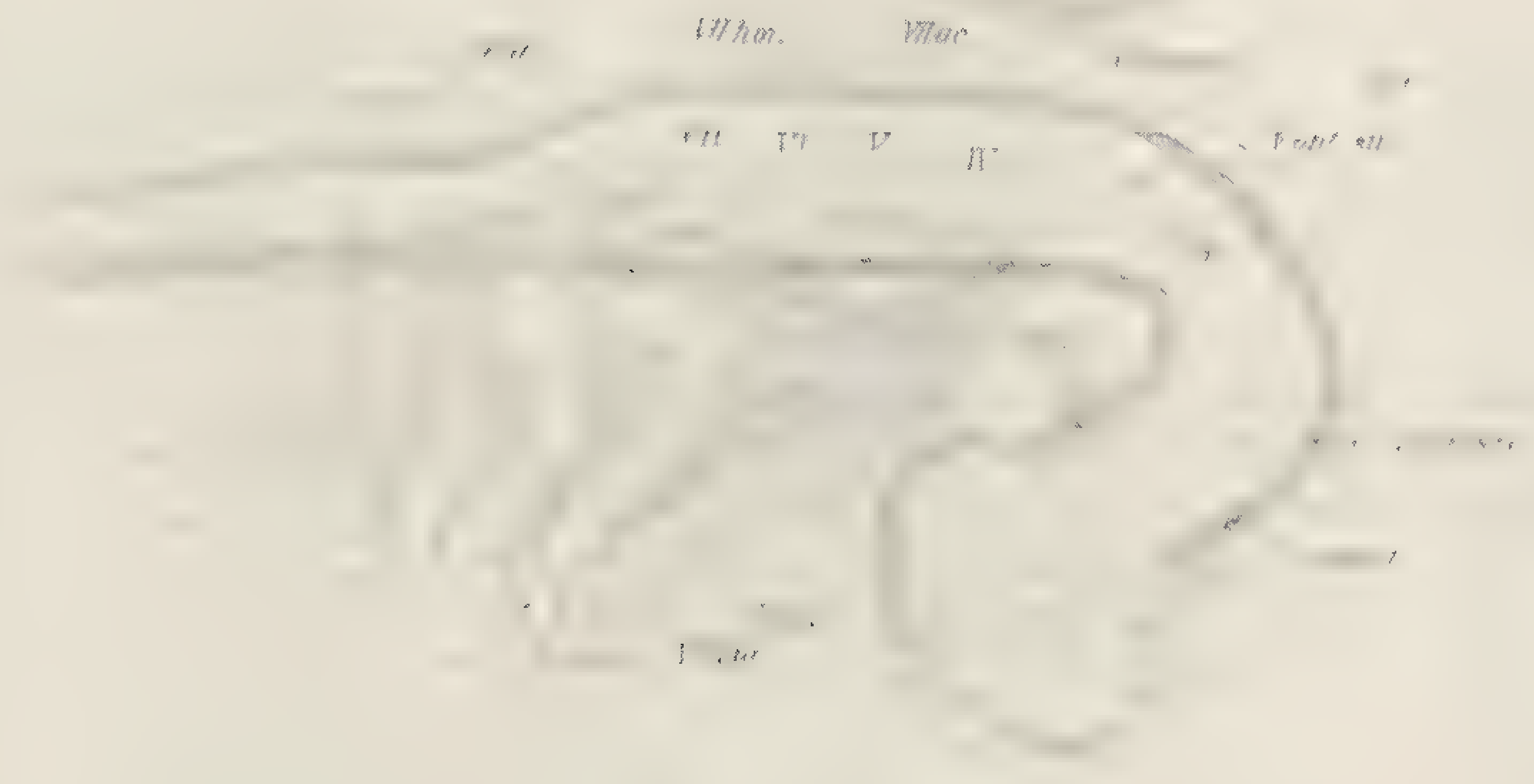
Fig. 18. An embryo with 52 somites (8 mm.). The otic capsule now lies opposite encephalomere VII. The thalamic and trochlear portions of the trigeminus appear only as scattered clumps of cells. Posterior commissure clearly differentiated. Between this and the preceding stage the oculomotorius has appeared as a fibrillar process from the ventral wall of the midbrain, near *gn. ms-ce.*

Fig. 19. An embryo with 65 somites (10 mm.). The chief peripheral branches of the cranial nerves have appeared; the abducens, as a process from the ventral wall of encephalomere VII.

Fig. 20. An embryo with 78 to 80 somites (16 or 17 mm.). In this stage the ramus opthalmicus superficialis trigemini appears to have fibrillar relation with the mesoderm of the 2d somite, which is growing forward. The fibrous process of the abducens has come into relation with the 3d somite, and also is seen to have a branch passing to the mesoderm posterior to its place of origin. Most of the fibres of the ramus mandibularis trigemini appear in connection with encephalomere III.

Fig. 21. An embryo 21 or 22 mm. long. The trochlearis is now differentiated, and in relation with the musc. obliquus posterior.


VII
VI
an.me.a


VII hm.
VIII ac
VII
VI
V
IV

21

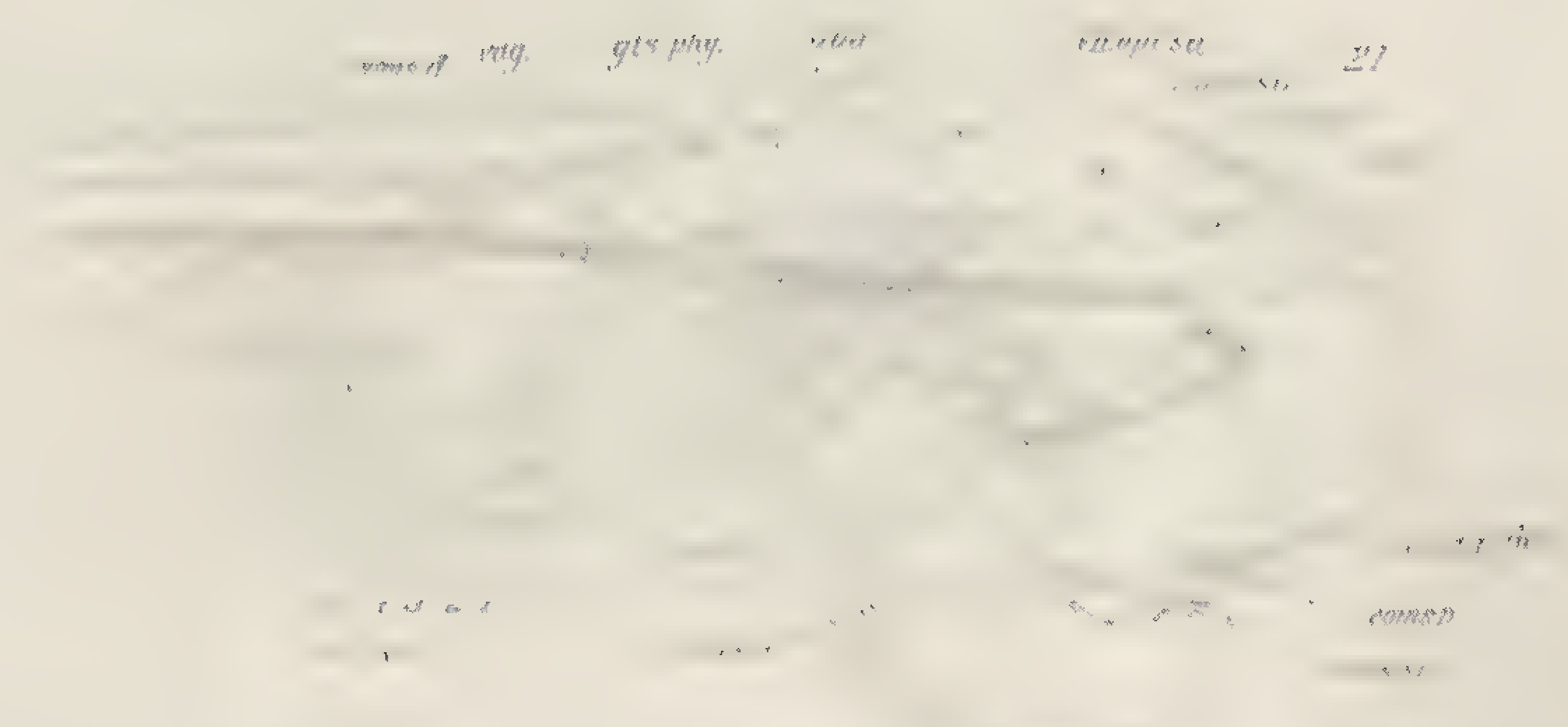

vag.
gls phy.
comsp

PLATE 5.

All the Figures except 31 and 32 represent frontal sections of embryos viewed from the dorsal side. All except Figures 25, 32, and 35 are magnified 43 diameters.

Fig. 22. A frontal section of an embryo with 14 or 15 somites. Encephalomere IV appears as a thickening of the lateral walls of the neural tube. No local thickening seen in the region of encephalomere III.

Fig. 23. From an embryo with 16 or 17 somites. A local thickening of the lateral walls in the posterior part of encephalomere III appears.

Fig. 24. From an embryo with 19 or 20 somites. The first four hindbrain neuromeres are now seen as local thickenings of the lateral walls, the thickening of neuromere III affecting its posterior part only.

Fig. 25. From an embryo with 28 to 30 somites, magnified 75 diameters. Five hindbrain neuromeres are seen. The auditory invagination appears opposite encephalomere VI.

Fig. 26. From an embryo with 50 somites (8 mm.) in the region of the "Deckplatte," showing the faintly marked expansions of the encephalomeres.

Fig. 27. A more ventral section of the same embryo. The encephalomeres sharply defined by constrictions. A secondary constriction in encephalomere III appears.

Fig. 28. A more ventral section of the same series, in the region of the lateral zones. The local thickenings of the encephalomeres well marked.

Fig. 29. A still more ventral section of the same embryo. The inner cusps between the neuromeres appear as in the more dorsal sections (Fig. 27).

Fig. 30. Frontal section in the region of the lateral zones of an embryo of 15 mm. The structure of the neuromeres is seen to be the same as that described by Orr ('87) for the Lizard.

Fig. 31. Cross section of an embryo with 20 somites, in the region of encephalomere IV, to show the thickening of the lateral zones.

Fig. 32. Cross section of an embryo with 28 to 30 somites in the posterior region of encephalomere III. The lateral zones more markedly thickened than in the previous stage (Fig. 31).

Fig. 33. Frontal section of an embryo with 50 somites (8 mm.), killed with a mixture of chromic, picric, and sulphuric acids, showing great intensification of the neuromeres, as the result of contraction due to inadequate fixation. The drawing, however, exaggerates the phenomena, since it represents the nuclear regions of the medullary wall with deeper shading.

Fig. 34. Frontal section of a 19-day *Swine* embryo. The constrictions between the neuromeres are sharply defined.

Fig. 35. Frontal section of an embryo of *Amblystoma* shortly after the closure of the neural tube. The neural tube is sharply outpocketed in the regions of proliferation of the ganglionic Anlagen of nerves V and VII. No evidence of a thickening or outpocketing comparable with encephalomere IV appears either at this or later stages.

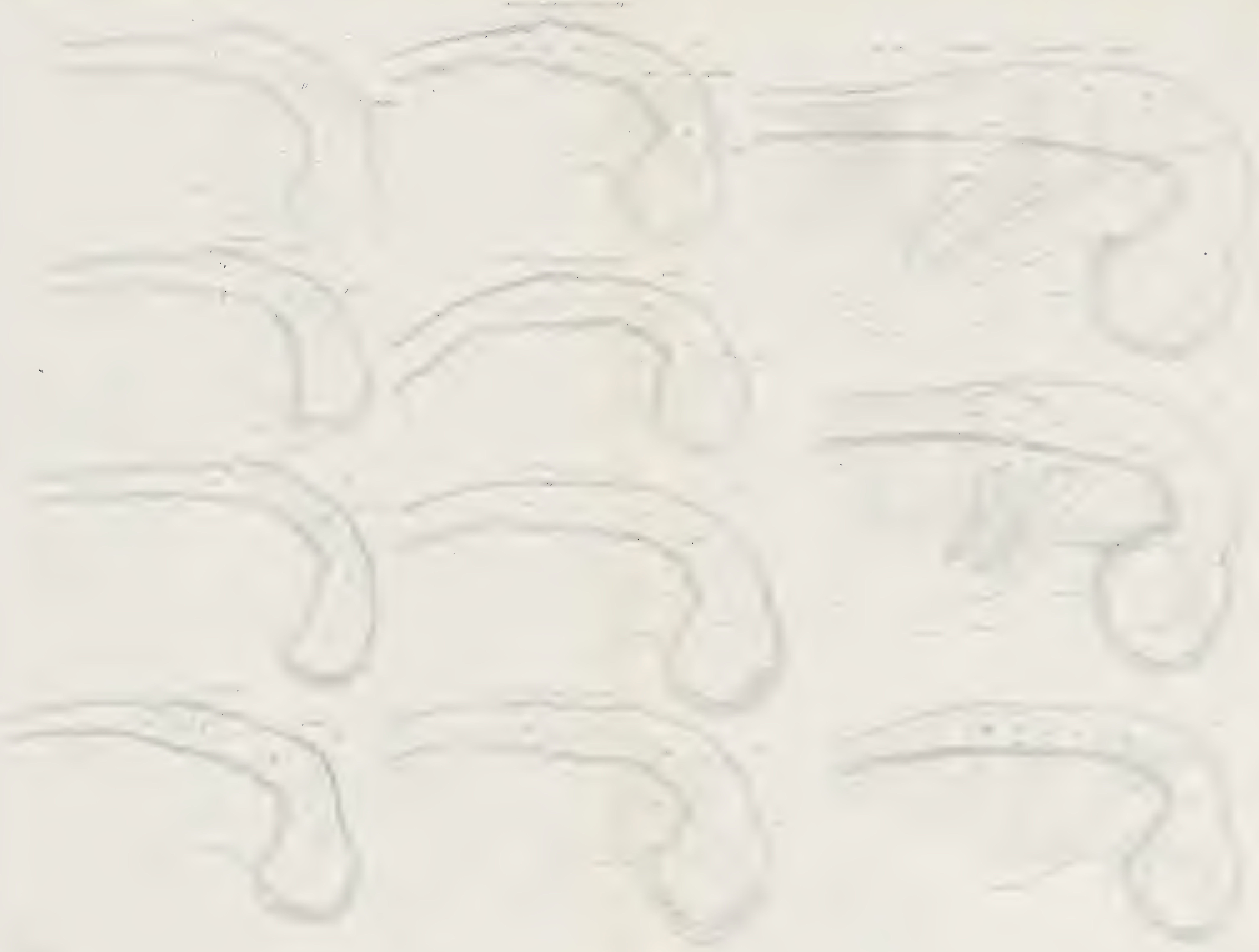


PLATE 6.

All Figures, except 40, magnified 100 diameters. Only the *right* half of the embryo is shown in Figures 36–39, 42, and 44.

Fig. 36. Frontal section of an embryo with 28 to 30 somites, showing the structure of the neuromeres IV and V in the region of the "Deckplatte."

Fig. 37. A more ventral frontal section in the same series cut in the region of the lateral zones. The neuromeres appear as well marked local thickenings. The radial arrangement of nuclei much less clearly shown than in the preceding section (Fig. 36).

Fig. 38. A still more ventral section of the same series, in the region of the "Grundplatte." The inner concavity appears as in the dorsal section (Fig. 36).

Fig. 39. Frontal section of an embryo with 28 to 30 somites, in the region of the trunk, showing the structure of the myelomeres and their relation to the somites.

Fig. 40. A reconstruction from sections and dissected specimens of the anterior end of an embryo with 28 to 30 somites, magnified 56 diameters. The lumen of the neural tube is exposed so as to show the hindbrain neuromere as local thickenings of the left wall. Van Wijhe's somites, at this stage separated by clearly marked constrictions, and Platt's anterior somite, are seen. Cells, in chief part derived from the neural crest, are seen surrounding the mesodermic epithelium of the 1st and 2d visceral arches.

Fig. 41. A cross section of an embryo with 28 to 30 somites in the trunk region. It is seen that the somites press against the ventral half of the neural tube. A migration of mesenchymatous cells from the sclerotome portion of the somite has already begun.

Fig. 42. Frontal section of an embryo with 50 somites (8 mm.) in the trunk region (ectoderm omitted), taken in the region of the points of exit of the ventral nerves. No constrictions in the ventral wall of the neural tube are to be seen at this stage, but the ventral nerves lie opposite the middle of the somites.

Fig. 43. A more dorsal frontal section from the same series as Figure 42. Constrictions in the lateral wall, opposite which the ganglia lie, show no corresponding ridges on the inner surface of the lateral wall.

VI
V
IV

PLATE 7.

Figures 44 to 53 illustrate the primary and secondary subdivisions of the forebrain and midbrain (encephalomeres I and II). All the Figures, except 47, 48, 53, 55, and 56, magnified 43 diameters.

Fig. 44. A parasagittal section of a *Chick* embryo of 33 hours' incubation (14 somites). Seven primary expansions of the encephalon appear, from the fifth of which, as in Squalus, the Anlage of the acustico-facialis is proliferated.

Fig. 45. A parasagittal section of a Squalus embryo with 18 somites. Six primary vesiculations (encephalomeres) are seen, all included in the region of the cephalic plate. Clefts in the dorsal mesoderm separate from each other all of van Wijhe's somites except the 4th and 5th.

Fig. 46. A parasagittal section of a Squalus embryo with 28 to 30 somites. Both encephalomeres II and III have become subdivided by constrictions, that of the former, however, affecting the ventral wall only. All of van Wijhe's somites separated by clearly marked mesodermic clefts.

Fig. 47. A parasagittal section of an embryo with 65 somites, magnified 23 diameters. Two subdivisions of encephalomeres I and three subdivisions of encephalomere II appear. The latter remains, however, dorsally a simple expansion. Nerve relation of encephalomeres II and VII with somites 1 and 3 shown.

Fig. 48. A frontal section in the dorsal part of encephalomeres I and II of an embryo with 30 to 32 somites, magnified 56 diameters. Only two vesiculations appear. Relation of thalamic portion of the trigeminus Anlage to these shown.

Fig. 49. Frontal section in the dorsal portion of encephalomeres I and II in an embryo with 19 or 20 somites. Two vesiculations only appear.

Fig. 50. A frontal section of the same embryo as that shown in Figure 48, but more ventral, showing the constriction in the ventral wall of the midbrain.

Fig. 51. A frontal section of an embryo with 65 somites in the dorsal part of encephalomeres I and II (forebrain and midbrain), showing subdivision (thalamic) of the former.

Fig. 52. A more ventral frontal section in the same series, showing a constriction in the lateral wall of the midbrain corresponding in position with the posterior commissure (*coms. p.*). The constriction in the forebrain corresponds with the superior commissure.

Fig. 53. A frontal section, showing forebrain and midbrain regions in an embryo of 22 mm., magnified 23 diameters. Two constrictions only appear, one in the region of the superior commissure, and the other in the region of the posterior commissure.

Fig. 54. A cross section of an embryo with 6 or 7 somites in the region of the cephalic plate, showing the ventral flexure of its edges.

Fig. 55. A cross section of an embryo at a stage when the edges of the neural plate are about to be raised, showing the differentiation of a neural crest in the anterior part of the cephalic plate. Magnified 100 diameters.

Fig. 56. A cross section in the posterior part of the cephalic plate of an embryo with 9 or 10 somites, showing that migration of neural-crest cells has already begun. Magnified 85 diameters.

PLATE 8.

Stages in the development of the nerves oculomotorius, ramus ophthalmicus superficialis trigemini, and ramus ophthalmicus profundus trigemini.

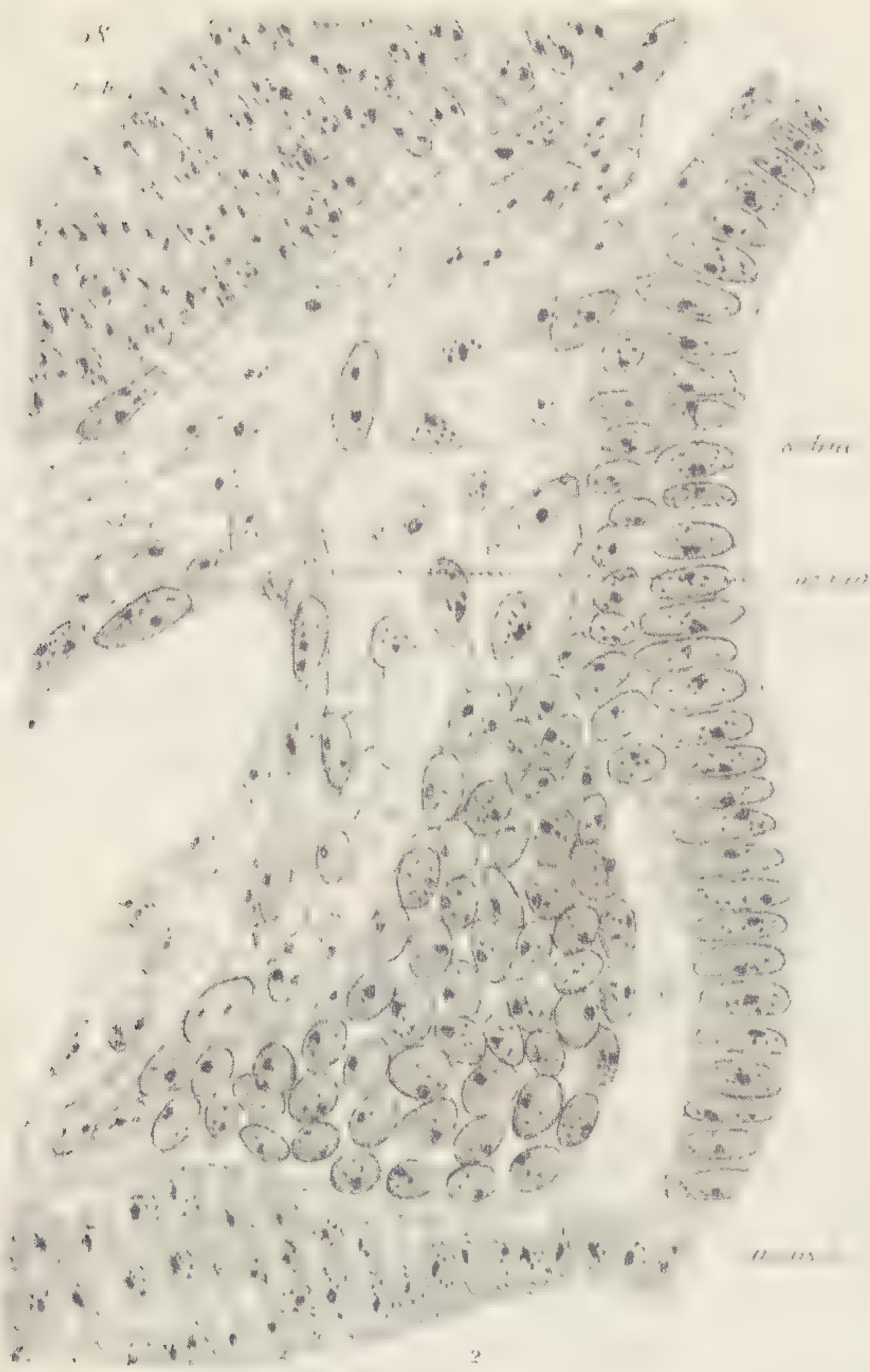
Fig. 58. A frontal section of an embryo with 55 somites ($8\frac{1}{2}$–9 mm.). Embryo killed with Davidoff's fluid. The oculomotorius appears as a cellular strand extending from the inner side of the mesocephalic (profundus) ganglion to the wall of the midbrain. Magnified 500 diameters. Reconstructed from three sections.

Fig. 59. A sagittal section of an embryo with 56 somites. Embryo killed with Davidoff's fluid. Near the brain the nerve appears composed of loose fibrillæ, while peripherally it is cellular in appearance. Magnified 360 diameters. Reconstructed from five sections.

Fig. 60. A combination of two parasagittal sections through the left side of an embryo of 16 mm. Protoplasmic processes from the ramus ophth. sup. trig. appear in relation with the anterior projection of the 2d cavity (musc. obl. superior). Magnified 70 diameters.

Fig. 61. A parasagittal section from the right side of an embryo with 51 or 52 somites (8 mm.). A well marked fibril passes from the mesocephalic ganglion to van Wijhe's 1st somite. The oculomotorius has not yet appeared.

58



59

60

gn Gas
gn ms ce
opt n lad

61

PLATE 9.

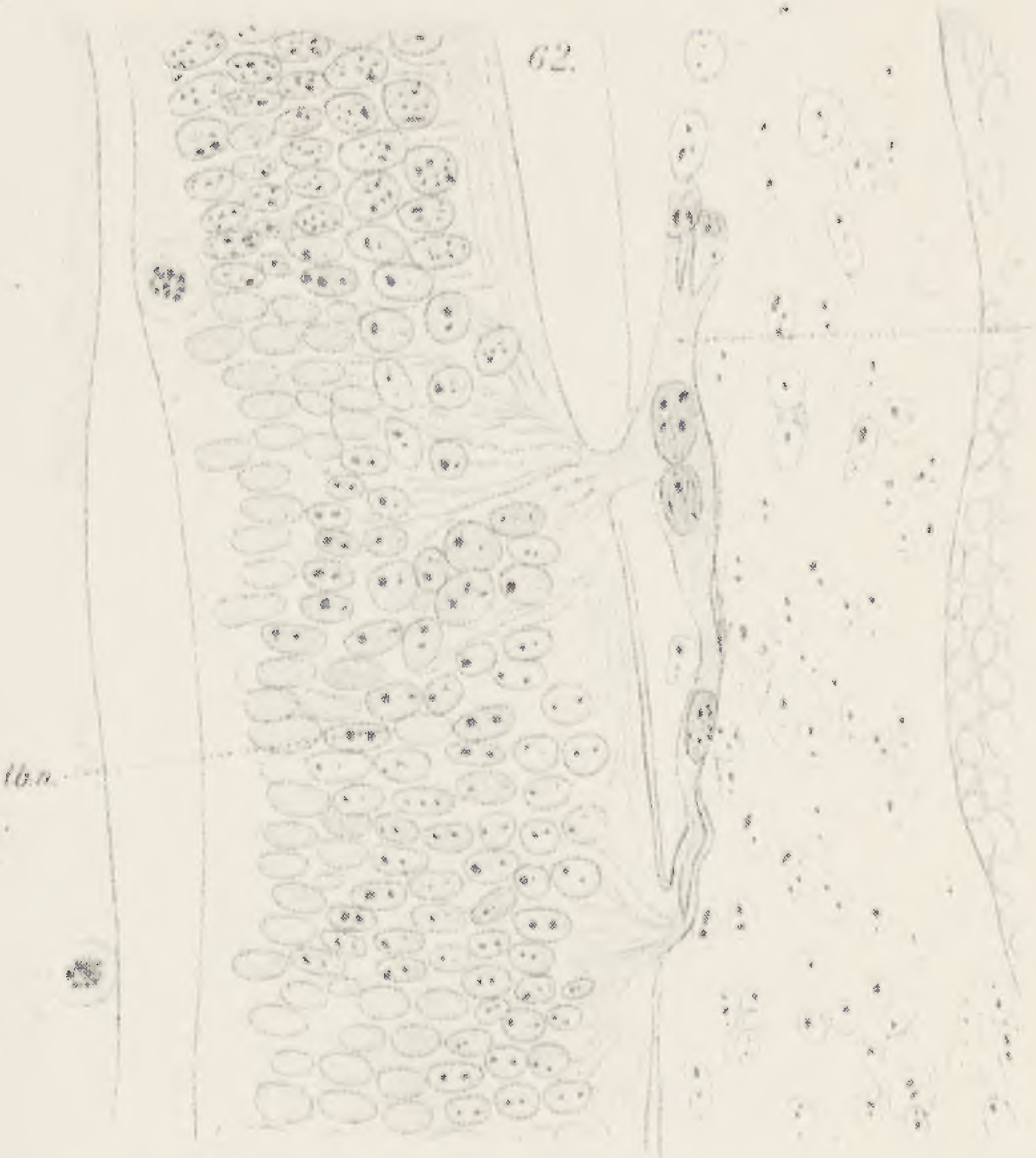
Stages in the development of the abducens nerve. All the specimens were killed with Davidoff's fluid (corrosive-acetic). All Figures are from frontal sections except Figure 65.

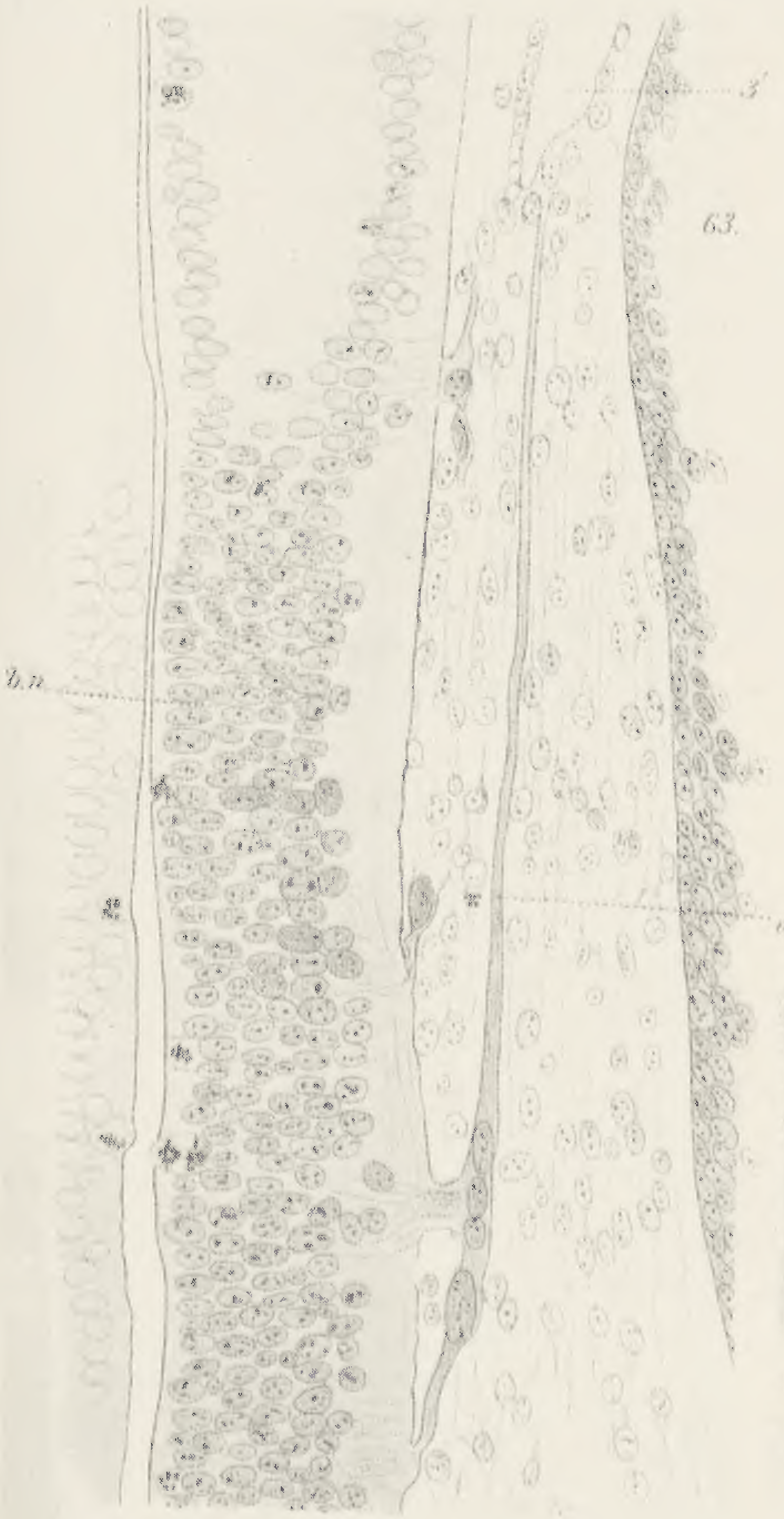
Fig. 62. A frontal section of an embryo with 62 somites (9 mm.). Magnified 450 diameters. Two roots are present.

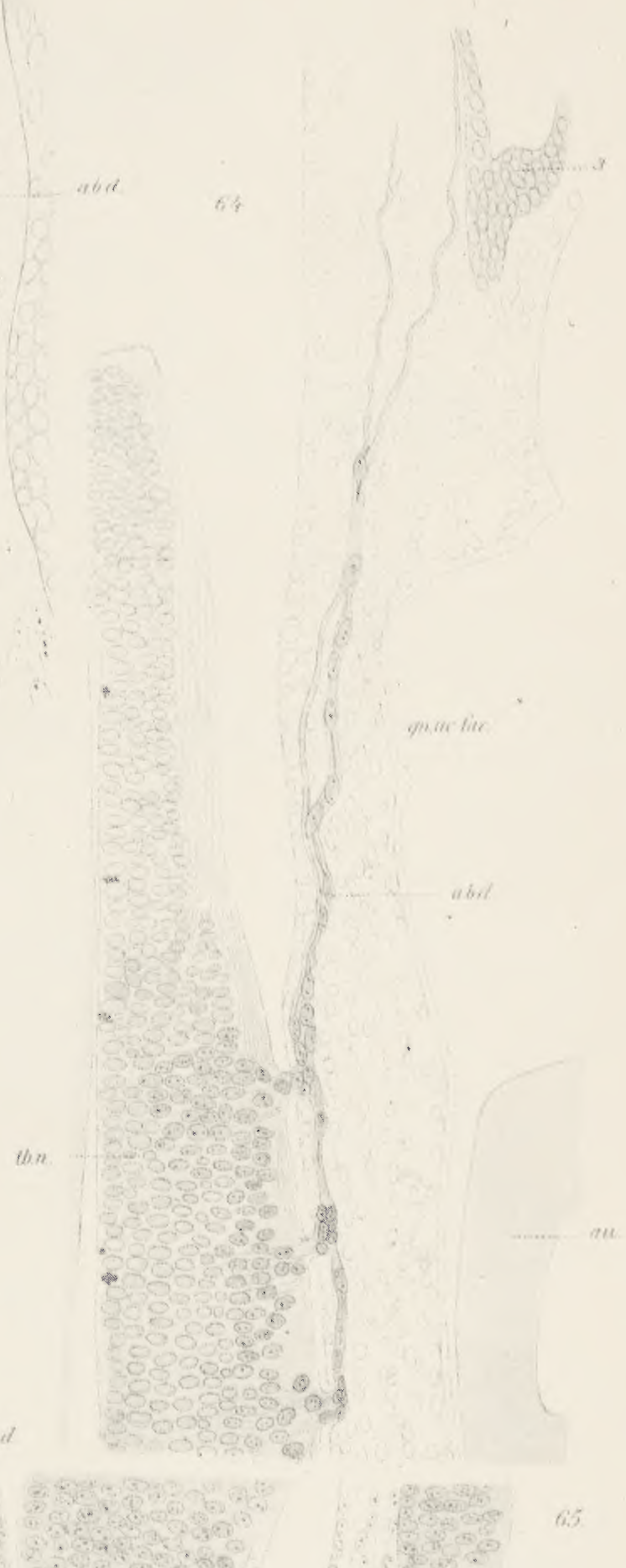
Fig. 63. From an embryo with 68 somites (10 mm.) magnified 285 diameters. The course of the nerve is very direct in this stage, at least in the specimen figured. Throughout the most of its course it is entirely free from nuclei.

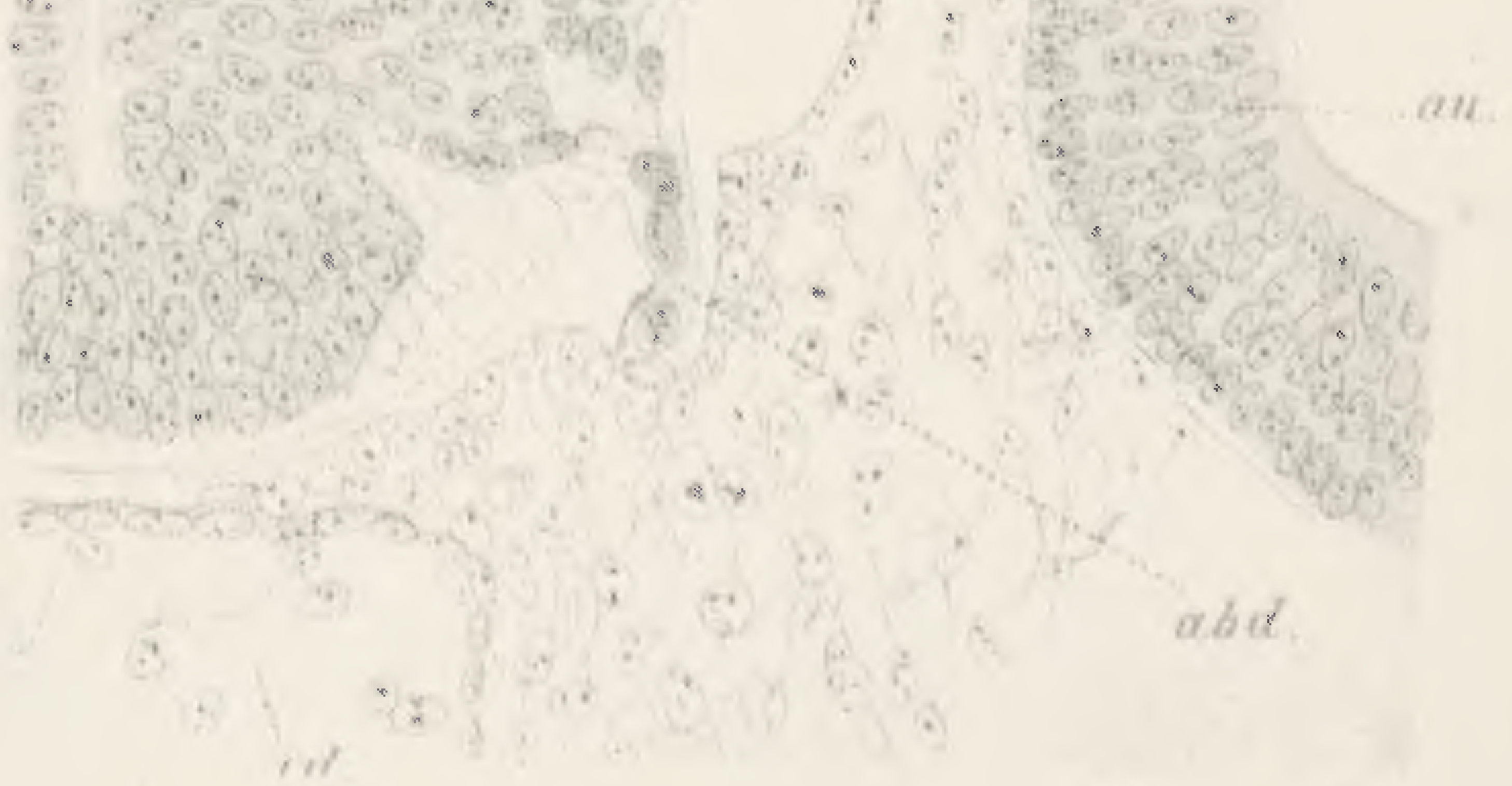
Fig. 64. A combination from 7 sections of an embryo with 80 somites. Three roots present on the side of the embryo figured. Deeply staining nuclei appear in close connection with the nerve, and there is some (in my opinion doubtful) evidence of the migration of nuclei to or from the neural tube. Peripherally the nerve divides into fine fibrillæ. Magnified 200 diameters.

Fig. 65. A cross section of an embryo with 75 somites in the region of the posterior root of the abducens, magnified 285 diameters. Evidence of migration of nuclei (?).


62.


63.


64.
3
gn.vc.fac.
abd
th.n.
au.


65.

H.V.Neal del. B. Meisel, lith. Boston